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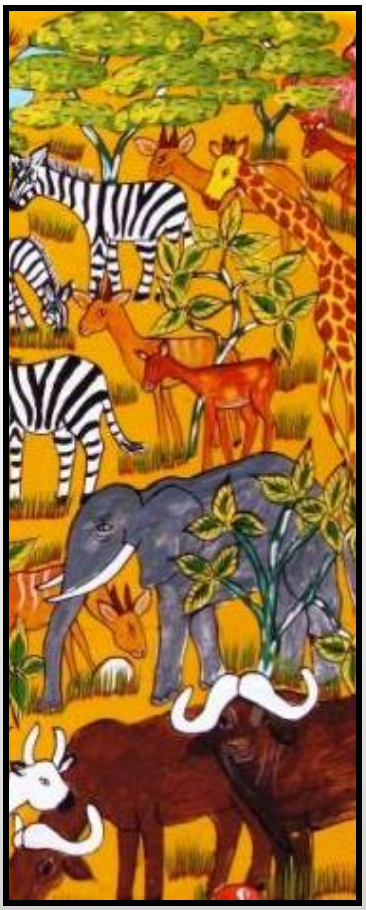

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Présentée par **Hugo Valls Fox**

To drink or not to drink?

The influence of resource availability on elephant foraging and habitat selection in a semi-arid savanna

Boire ou ne pas boire?

De l'influence de la disponibilité en ressources sur l'approvisionnement et la sélection de l'habitat des éléphants dans une savane semi-aride

Soutenue le 14 décembre 2015 devant le jury composé de

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PhD Thesis

Hugo Valls Fox

2015 - Université de Montpellier

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Je m'occupe des éléphants. […] Je me contente de vivre parmi eux. Je passe des mois entiers à les suivre, à les étudier. A les admirer, plus exactement. A ne vous rien cacher, je donnerais n'importe quoi pour devenir un éléphant moi-même.

I care for elephants. […] I am content with living among them. I spend entire months following them, studying them. Admiring them, more exactly. Honestly speaking, I would give anything to become an elephant myself.

Romain Gary, Les Racines du ciel, 1956

General introduction

Figure 1: Elephant family groups aggregate to drink at sundown, Nyamandhlovu pan (the place of many elephants), Hwange National Park, Zimbabwe.

1 Surface water and resource use in semi-arid ecosystems

1.1 Water: a key limiting resource

Water is an essential constituent of all living organisms; it is a key resource in many ecosystems where access to water can determine individual fitness and ultimately population abundance. In arid and semi-arid ecosystems, organisms have adapted their life histories to cope with water scarcity. Annual plants can sustain prolonged periods of dormancy, as seeds that germinate, grow and reproduce within the short period following rainfall events. Perennial plants can become dormant by storing their reserves below ground or overcome water scarcity by sending roots to tap into buried aquifers up to 40m below ground. Some animal species have also adapted dormancy strategies, others have acquired physiological and behavioural adaptations that enable them to survive without access to drinking water (Kay 1997; Fuller et al. 2014). For instance, large herbivores can fulfil a significant proportion of their water requirements by extracting water from the vegetation they eat. Several browser

species have been considered as water independent because the foliage they consume contains sufficient moisture all year around to satisfy their requirements and their movements are not restricted by the distribution of drinking water (Redfern et al. 2003). However, grazing fodder dries out rapidly during the dry season, as a result most grazing species water requirements increase (Scheibe et al. 1998) and their range is limited by surface water availability (Western 1975; Redfern et al. 2003).

Water limitation can determine survival and reproductive success. For instance, experimental studies on rodents revealed water requirements more than double during lactation (Smith & McManus 1975) and limited access to water substantially reduces short and long term reproductive success (Scribner & Wynne-Edwards 1994). The direct effects of water limitation may be relevant for species living in arid environments that extract water from their food (Nagy 1994) or need to dig their way to underground seeps (Rozen-Rechels et al. 2015). However, when animals have access to drinking water, they can fulfil their requirements within a few minutes (Valeix et al. 2008a) and the absolute quantity of available water may be less limiting than the spatiotemporal constraints associated with access to free standing water sources. Unlike foraging resources, water does not limit animal populations per se. In the case of large mobile herbivores living in seasonal environments such as savannas, the distribution of surface water limits the area herbivores can exploit and ultimately the quantity of available forage. Water indirectly limits large herbivore populations by limiting the area they can access during a critical time of the year, thus determining the total amount of available food which in turn governs the level at which density dependent processes occur (Walker et al. 1987; Illius & O'Connor 2000; Chamaillé-Jammes et al. 2008). Density dependence occurs via a reduced juvenile survival (Bonenfant et al. 2009), particularly during droughts (Hillman & Hillman 1977; Walker et al. 1987; Duncan et al. 2012) although droughts may also incur excess mortality for all age classes (Walker et al. 1987; Dudley & Criag 2001). Water scarcity may depress juvenile survival because lactating females drink more often (Adams & Hayes 2008) and must therefore remain closer to water sources than non-reproductive individuals (Rubenstein 2010).

1.2 The effects of water: from foraging decisions to landscape use

Co-limitation by multiple resources implies trade-offs in the acquisition of each resource. In the case of surface water and forage, these trade-offs emerge from the heterogeneous distribution of water in time and space (Gaylard, Owen-smith & Redfern 2003). When water sources are scarce and far apart, water dependent animals can be assimilated to central place foragers making foraging excursions between drinking bouts (Olsson, Brown & Helf 2008). However, true examples of central foraging around water points may be restricted to domestic livestock kept in paddocks (Squires 1976) with a single water source or herded by people (Coppolillo 2001; Butt 2010). Free ranging herbivores are more likely to be multiple central place foragers because they have access to multiple central places (Chapman, Chapman & McLaughlin 1989). Finally, the distance between different water sources may vary. Landscape complementation occurs when water sources are in close proximity enabling

individuals to exploit their foraging resources more efficiently (Dunning, Danielson & Pulliam 1992). Central place foraging, multiple central place foraging and landscape complementation provide a hierarchical framework to assess limitation by two non-substitutable resources (Figure 2).

1.2.1 Central place effects

Central place effects occur when animals must return regularly to a single location in the landscape between foraging trips. The main assumption made by central place foraging models is that exploiting resource patches further away from the central place is more costly. The nature of the cost may be increasing predation risk or travel costs with distance from the central place (Olsson, Brown & Helf 2008), limited oxygen reserves for diving animals while foraging underwater (Parkes et al. 2002; Hoskins, Costa & Arnould 2015), or limited water reserves for water dependent herbivores (Chapter 2; Cain, Owen-Smith & Macandza 2012). Central place effects depend on the type of central place the animal is returning to. For instance, if the central place provides a refuge from predators such as a nest, a burrow, or a kraal in the case of domestic livestock (Kuiper et al. 2015), predation risk will increase with distance from the refuge (Olsson, Brown & Helf 2008). However, when the central place is a resource such as a waterhole (Davidson et al. 2013) the central place forager might alter its use of the central place to reduce the likelihood of encountering a predator (Valeix et al. 2009; Courbin et al. 2015).

One of the key consequences of central place effects is the emergence of a resource gradient due to depletion close to the central place. For example, fish densities are lower around seabird colonies (Birt et al. 1987) and forage biomass is lower on prairie dog *(Cynomys ludovicianus)* towns than the surrounding grasslands (Augustine & Springer 2013). Central place effects associated with strong density dependence effects (Rozen-Rechels et al. 2015) may ultimately regulate population size (Gaston, Ydenberg & Smith 2007). The area affected by herbivores around water points has been termed piosphere (from the Greek “pios” to drink; Lange 1969). In addition to seasonal depletion, piosphere effects include long term modifications of the vegetation structure and composition along a distance to water gradient (Thrash & Derry 2008; Chamaillé-Jammes, Fritz & Madzikanda 2009; Landman et al. 2012). Overall, piosphere effects entail a resource gradient from the central place water source towards the periphery.

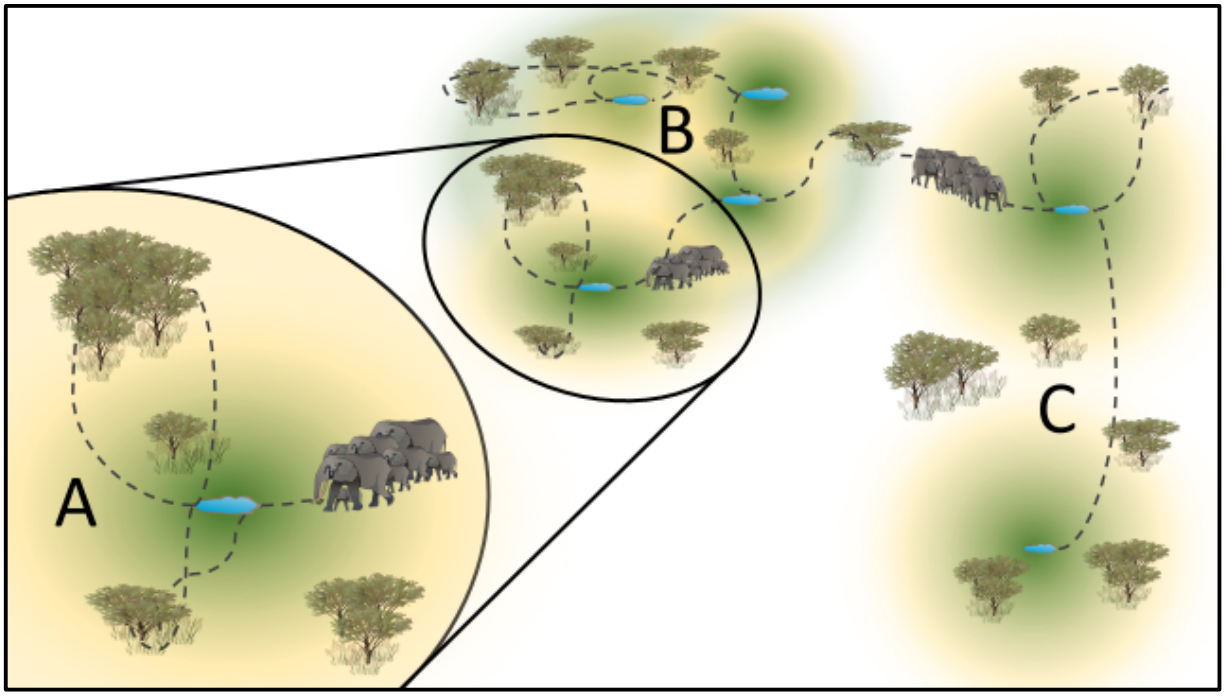


Figure 2: The effects of heterogeneous resource distribution on foraging and habitat selection. (A) Central place foraging effects around a single water pan. Multiple central place effects (B & C) depend on larger scale processes such as resource complementation in areas with higher waterhole density (B).

During each foraging trip, herbivores have a limited amount of time to forage before they must return to the central point. As a result, foraging decisions are driven by missed opportunity costs. Accordingly, herbivores spend more time foraging and have lower giving up densities further away from water where forage is more abundant than close to water where it is scarce (Shrader et al. 2008, 2012). Foraging trips are thus characterized by greater travelling speed at the beginning and the end of the trip (Squires 1976; Chamaillé-Jammes et al. 2013). Accordingly, feral horses on Sable Island, Canada, select for high quality grasslands away from water ponds and lower quality heathlands close to water ponds due to forage depletion of high quality grasslands close to water ponds (Rozen-Rechels et al. 2015). However, horses that must dig for their water spend more time accessing water than horses drinking at ponds. These horses have less foraging time and select more strongly for low quality heathlands close to water suggesting stronger density dependence when time allocated to acquiring water increases (Rozen-Rechels et al. 2015). The trade-off between water and forage requirements provides a good case study to understand the central place effects of non-substitutable resources. In chapter 2, we explore to what extent African elephants use their locomotional and navigational capacities to solve the trade-off imposed to central place foragers confronted with resource depletion (Gaston, Ydenberg & Smith 2007; Chamaillé-Jammes *et al.* 2008).

1.2.2 Multiple central place effects

A central place forager is constrained by the distance it can travel between visits to the central place and may be forced to reduce its total intake (Squires & Wilson 1971). The use of multiple central places allows an individual to expand its home-range by changing central place (Chapman, Chapman & McLaughlin 1989) and reduces travel cost to the central place (McLaughlin & Montgomerie 1989, Figure 1). Chamaillé-Jammes et al. (2013) distinguished looping trips (the individual returns to the same central place) from commuting trips (the individual changes central place). Looping trips can be analysed within a classical central place foraging framework (chapter 2 & 3) whereas commuting trips result from a mixture of lower and higher order decisions that have not been explicitly addressed in these studies. Surprisingly, multiple place central foragers do not necessarily go to the central place that is closest to their previous or next foraging location (Chapman, Chapman & McLaughlin 1989; Chamaillé-Jammes *et al.* 2013) suggesting the quality of the central place or social interactions may also play a role in higher order movement decisions.

1.2.3 Landscape complementation effects

Landscape complementation occurs when non-substitutable resource patches are sufficiently close to one another for animals to successfully exploit them (Dunning et al. 1992, Figure 1). The key notion underlying landscape complementation is proximity. For instance, wild pigs living in riverine systems in Australia depend on pastures for forage and riverine woodlands for refuge. Population rate of change was greater for pigs using pastures close to riverine systems resulting from increased foraging efficiency (Choquenot & Ruscoe 2003). Similarly, in Bialowieza Forest, Poland, ravens *(Corvus corax)* build their nests in coniferous stands but forage in deciduous woodlands and open areas. As a result, breeding performance was higher for couples living in coniferous stands which were close to large areas of their preferred foraging habitats (Mueller et al. 2009). In both of these studies, landscape complementation depended on the location of individual home-ranges. Individuals living in areas with greater resource complementation had a higher reproductive success (Mueller et al. 2009) and populations exhibited positive rates of increase (Choquenot & Ruscoe 2003). However, landscape complementation effects have also been found within an animal's individual home-range such as the selection of refuge areas (Hoglander et al. 2015).

Habitats comprising non substitutable resources and located in close proximity to one another have also been defined as key habitats that are used disproportionately to their availability in the landscape (Scoones 1995). As a result, these areas are more susceptible to depletion with subsequent density dependence effects (Walker et al. 1987). This implies a paradox, by which habitats with high resource complementation (i.e. close to water) may be selected as a result of complementation and avoided because of forage depletion. However, the scale at which water sources attract or repulse herbivores may differ. Although scaling effects have been widely acknowledged in habitat selection studies (De Beer & Van Aarde 2008; Harris et al. 2008; Marshal et al. 2010; de Knegt et al. 2011; Shrader et al. 2011), to my knowledge a single

study has attempted to account for this paradox (Roever et al. 2014). In their study on elephant habitat selection, Roever et al. (2014) demonstrate that the distinction between different movement modes reveals fine scale patterns of avoidance of waterholes. Habitat selection models with the same predictor variables that made this distinction found no patterns or the opposite pattern of preference of areas close to water. The consequences of resource depletion on central place effects and landscape complementation effects are explored in chapter 3 of this thesis and the distinction between foraging bouts serve as a baseline in habitat selection analyses conducted in chapter 4.

1.3 The effects of seasonal changes in water availability

Landscape composition (patch quality) and physiognomy (patch disposition) provide a template to understand animal use of multiple resources (Dunning, Danielson & Pulliam 1992). For water dependent herbivores, landscape composition can be summarized by forage quantity, phenology and quality whereas landscape physiognomy is described by distance to water and waterhole density. Savanna systems are characterized by strong seasonal variations in both of these landscape attributes. During the dry season, overall patch quality decreases and water pans dry up. Changes in composition are not uniform since depletion preferentially occurs close to water (Thrash & Derry 2008). As a result, landscape complementation decreases, and the trade-off between satisfying their water and their feeding requirements increases in central or multiple central place foragers. Seasonal variation in landscape properties are also accompanied by seasonal changes in abiotic conditions such as ambient temperature which is one of the major drivers of water requirements in living organisms.

Animals living in arid and semi-arid rangelands respond to seasonal variation by altering their movement patterns. For example, free ranging domestic sheep increase the frequency of visits to water and distance travelled during the dry season (Daws & Squires 1974). However in an experimental setting, when forced to travel further to obtain their forage, sheep reduce their drinking frequency and forage intake. Yet, they partially compensate for lower drinking frequency by increasing water intake at each visit (Squires & Wilson 1971). Thus, herbivores can increase their movement rate to visit water more often up to a given threshold (14km/day in the case of sheep). Beyond that threshold herbivores may concomitantly reduce their intake of water and forage to suboptimal values in order to reduce travel costs (Squires & Wilson 1971). Furthermore, reduction of food intake can be used as a means of water conservation (McFarlan & Wright 1969).

Box 1: Temperature and the physiological effects of water requirements on movement.

Water requirements increase with ambient temperature (Dunkin *et al.* 2013). Herbivores can increase their water intake by increasing the frequency of visits to water (Squires 1976; Adams & Hayes 2008) or water consumption at each drinking bout (Daws & Squires 1974). However there are alternative strategies to reduce evaporative water loss such as:

- Allowing body temperature to rise (Fuller *et al.* 2014; Hetem *et al.* 2014).
- Reducing daytime activities and increasing nighttime or crepuscular activities (Daws & Squires 1974; Owen-Smith 1998; Maloney *et al.* 2005; Aublet *et al.* 2009).
- Selecting cooler habitats, sometimes at the expense of foraging opportunities (Kinahan, Pimm & van Aarde 2007; Aublet *et al.* 2009; van Beest, Van Moorter & Milner 2012).
- Selecting forage with higher moisture content (Jarman 1973; Macandza, Owen-Smith & Cain III 2012).

From a researcher's perspective, seasonal changes in environmental conditions (i.e. ambient temperature), landscape composition and physiognomy offer a unique opportunity to quantify how herbivores solve the trade-off between drinking and foraging. These seasonal changes have been the backbone of our investigation.

1.4 Does risk affect waterhole use or water distribution alter the perception of risk?

Key resources such as waterholes may be critical habitats regarding animal response to disturbances. Water dependent species need to drink regularly and perceive waterholes as risky habitats due to greater predation risk (Valeix et al. 2008c; Periquet et al. 2010). For example, herbivores that usually visit waterholes during the day in protected areas (Valeix, Chamaillé-Jammes & Fritz 2007) come to drink at night in trophy hunting areas (Crosmary et al. 2012b) or in the evening in areas used by cattle (Kangwana 2011). In addition to spatial costs, animals increase vigilance in habitats perceived as risky (Crosmary et al. 2012a) or when confronted to a disturbance (Pangle & Holekamp 2010).

At the boundary of protected areas, proximity to humans can be perceived as risky by animals (Kangwana 2011). Anthropogenic activities can alter animal activities in space and time. Animals may avoid people at large scales (Hibert et al. 2010), particularly close to water sources (De Leeuw et al. 2001). At finer spatiotemporal scales, animals typically avoid areas used by people during the day and may exploit them more intensively at night (Hebblewhite & Merrill 2008; Graham et al. 2009; Marchand et al. 2014). In chapter 4, we explore the influence of surface water availability on herbivore avoidance of cattle, an indicator of human activity, at the boundary of a protected area.

1.5 Hwange National Park: a water dependent ecosystem.

One of the challenges of field based ecological studies is to disentangle the multiple factors that drive ecosystem functioning. Major advances in ecological theory have emerged from the study of simple and apparently atypical ecosystems. Hwange National Park, in North western Zimbabwe, is one of such systems for those who wish to study the influence of surface water, a key yet sparsely distributed resource (box 2). One of the main features of Hwange NP is the absence of perennial rivers and the near absence of any kind of perennial water source throughout most of the park.

The climate in Hwange is typical of semi-arid savannas; water is plentiful and widespread during the 4-5 month long rainy season. Yet, once the 7-8 month long dry season starts, animals can only find water in a few remaining water pans. Water pans are shallow depressions ranging from a few dozen to a few hundred meters wide that fill with water during the rainy season (Figure 3). Natural pans dry up during the dry season but can be supplemented by pumping from a nearby borehole. During the dry season, water dependent species come to water regularly to drink (Hayward & Hayward 2012) and travel away from water to forage. Unlike rivers, that provide numerous drinking locations, water pans can be seen as true central places (Figure 2).

African elephants *(Loxodonta africana)*, are by far the most abundant herbivore living in Hwange National Park, and account for 80-90% of the total herbivore biomass (Fritz et al. 2011). Elephants are particularly good candidates to study the constraints of surface water. They are water dependent and must return to water regularly to drink (Chamaillé-Jammes et al. 2013) . Elephants consume large amounts of browse during the dry season. Unlike riparian forests and floodplains on the banks of perennial rivers, the vicinity of water pans provides very little forage to elephants within a radius of a few hundred meters as a result of piosphere effects (Thrash & Derry 2008). As a result, unlike other herbivore species, such as zebra that spend most of the day in the open areas surrounding water pans, elephants in Hwange NP only visit water pans briefly to drink before getting away from water to forage. This characteristic is essential to distinguish the use of both drinking and foraging resources in time and in space thus providing the template to measure central place effects. Finally, elephant densities during the dry season are amongst the highest in the world (Chamaillé-Jammes et al. 2014) (see Box 3 for a historical perspective). Their population is believed to be regulated by density dependence effects associated with surface water distribution (Chamaillé-Jammes et al. 2008). Thus, our study of African elephant's use of water pans in Hwange will investigate some of the potential movement constraints and landscape effects of surface water distribution underlying these density dependence effects.

Box 2: Hwange National Park: A semi-arid woodland savanna.

- **Location:** Latitude: 19°S, Longitude: 26°E. North-Western Zimbabwe, Africa.
- **Area:** 14 650 km^2.
- **Climate:** Semi-arid, mean annual rainfall (600mm), 98% of precipitation falls between November and April (rainy season Temperatures range from 0°C to 25°C during the cold dry season in June to 15°C to 35°C during the hot dry season in October.
- **Geology:** A central plateau encompassing two thirds of the park is covered by Kalahari sands, the North and extreme South consist in eroded granites, gneiss and basalts.

Figure 3: Elephant bull drinking at a natural water pan, April 21st 2013

- **Surface water:** Perennial Rivers are absent, seasonal rivers in the North and thousands of temporary pans hold water during the rainy season and dry-up during the dry season. Approximately 60 permanent waterholes are maintained by pumps throughout the dry season.
- **Vegetation:** Dystrophic savanna woodland and bushland dominated by *Acacia spp., Baikiaea plurijuga, Colophospermum mopane, Combretum spp. & Terminalia spp.*
- **Wildlife:** Dominant herbivores include African savanna elephant *(Loxodonta africana)*, giraffe *(Giraffa camelopardalis),* African buffalo *(Syncerus caffer),* greater kudu *(Tragelaphus strepsiceros),* plain zebra *(Equus quagga),* impala *(Aepyceros melampus)*, and warthog *(Phacochoerus africanus).* Carnivores include lion *(Panthera leo)*, spotted hyena *(Crocuta crocuta),* leopard *(Panthera pardus),* cheetah *(Acynonyx jubatus),* and wild dog *(Lycaon pictus).*

Box 3: A brief history of Hwange National Park elephants and water availability.

- ***19th Century:*** Intensive hunting by European hunters throughout Southern Africa progressively shifted northward following the decimation of South African populations by the early 1800's. In the mid-19th century, 2000-3000 were killed annually in the neighboring areas corresponding to present day Botswana. By the turn of the 20th century elephants had been exterminated from most of the region, small numbers remained in isolated pockets such as the area covered by present-day Hwange National park (Vandewalle & Alexander 2014).
- ***1928***: Proclamation of the Wankie Game Reserve, less than a thousand elephants in the Reserve (Davison 1967).
- **1936:** First windmills erected to supply water and effective protection enforced. However elephants do not stay during the dry season due to lack of water. (ibid.)
- **1940's**: First diesel pumps provide reliable water supply throughout the dry season. The number of pumped pans increases gradually up to about 60 pumped pans in the 1980's. (Chamaillé-Jammes *et al.* 2014)
- **1930-1966** Elephant population increases exponentially (5%/ year) (Cumming 1981)
- **1966:** Start culling program. A threshold of 13000 elephants was only defined in 1974 (ibid.)
- **1970's:** Population estimated at 14 000 elephants. (ibid.)
- **1983:** It is estimated there are more than 20 000 elephants. The major culls of 1984, 1985 and 1986 brought the population down to 13 000 (Cumming 1981).
- **1986**: End of culling operations. Elephant population doubled from 15 000 to 30 000 in a few years probably due to immigration from an unknown location (ibid.). However, elephant bulls are still shot in surrounding Safari Areas by trophy hunters or in Communal lands by competent authorities as Problem Animal Control (Guerbois 2012).
- **1992-present**: Elephant populations fluctuates around 35 000-45 000 individuals (Chamaillé-Jammes *et al.* 2008; Dunham 2015)
- **2000-2008:** Collapse of tourism and Hwange National Park revenues, the economic crisis results in an unquantified reduction of game water supply.
- **2008-2015**: Revival of the tourism industry. New waterholes are opened in private concessions. The occurrence of poaching events increases (particularly at the end of the dry season) but the number of animals lost remains low in comparison with the total estimated population.
- **2014:** Aerial population census of 45 846 ± 6 300 individuals (Dunham 2015)

2 The importance of resources in elephant natural history

2.1 Water dependence and thermoregulation

African savanna elephants are the largest extant terrestrial animal. Males average 3.2m in height and 6 tons in weight, females only average 2.6m in height and 2.8 tons in weight (Wittemyer 2011). Pronounced sexual dimorphism, habitat use and activity patterns of female and male elephants has led several authors to consider elephant bulls and family herds composed of adult females and their young as distinct ecological species (Shannon et al. 2006, 2008; Smit, Grant & Whyte 2007; de Knegt et al. 2011).

Thermoregulation in mammals is largely influenced by body size due to the constraints imposed by body surface to volume ratio. In tropical environments gigantic animals like elephants and other megaherbivores have higher baseline rates of metabolic heat production than heat loss (Rowe et al. 2013). Elephants have evolved a range of physical characteristics that increase heat dissipation: Large and highly vascularized ears (pinna) serve as thermal windows to evacuate excess heat (Phillips & Heath 1992, 2001; Weissenböck et al. 2010); their skin is more permeable to heat dissipation than other mammals (Dunkin et al. 2013) and even their body hair facilitates convective heat loss at the skin surface (Myhrvold, Stone & Bou-Zeid 2012). In addition, behavioural adjustments include wallowing, spraying and bathing (Weissenböck, Arnold & Ruf 2012). African elephants can consume up to 200L of water per day, although their water requirements largely depend on ambient temperature (Dunkin et al. 2013). Namib elephants can travel up to 4 days without drinking (Viljoen 1989). However, in Hwange National Park, elephants visit waterholes periodically every 5h, 24h, 48h or 72h (Chamaillé-Jammes et al. 2013). Elephants can reduce water loss by selecting habitats that maximize heat loss (Kinahan, Pimm & van Aarde 2007) and may adjust their activity patterns by shifting travelling at night (Wall et al. 2013).

2.2 Water dependence and foraging behaviour

African savanna elephants are mixed feeders with strong seasonal variations of their diet. Elephants can go from being nearly pure grazers during the peak of the rainy season to nearly pure browsers during most of the dry season (Williamson 1975a; Cerling et al. 2009). Several studies have reported elephants made hierarchical top-down habitat selection decisions by selecting better habitats at coarse scales (Marshal et al. 2010; Shrader et al. 2011). At finer scales, elephants will nonetheless prefer vegetation in nutrient hotspots such as termite mounds (Holdo & McDowell 2004). Elephants select areas with greener vegetation throughout the year (Loarie, Aarde & Pimm 2009; Bohrer *et al.* 2014), both forage water content and quality are strongly correlated to greenness, water supplementation cannot be distinguished from forage quality as a foraging criterion. During the rainy season, elephants are no longer constrained by surface water and may migrate to dryer areas that can provide better quality forage (Williamson 1975b; Cerling *et al.* 2006; Wall *et al.* 2013; Bohrer *et al.* 2014).

Elephants have also been reported to shift their dietary requirements from maximizing Nitrogen intake during the rainy season to maximizing energy intake during the dry season (Pretorius et al. 2012). During the dry season, elephants spend 17-19 hours a day foraging (Moss, Croze & Lee 2011) but lose body condition and face higher risks of mortality (Williamson 1975a; Conybeare & Haynes 1984). Surface water availability becomes a major determinant of habitat use during the dry season (Leggett 2006a; De Beer & Van Aarde 2008; Loarie, van Aarde & Pimm 2009; Cushman, Chase & Griffin 2010; Roever *et al.* 2014) as elephants remain within a few kilometres of water (Conybeare 1991; Redfern et al. 2003). Their use of waterholes is best described as multiple central place foraging characterized by directed movement at higher speed to and away from water (Chamaillé-Jammes et al. 2013; Polansky, Kilian & Wittemyer 2015). During the dry season, elephants are thus forced to remain close to water to drink (Conybeare 1991; Chamaillé-Jammes et al. 2013). Elephants with access to riparian areas or floodplains may remain there to forage, elsewise they will select areas away from water to forage (Roever et al. 2014).

In addition to water and high quality foraging areas elephant may also travel specifically to salt-licks or more saline pumped water pans in order to supplement their diet in sodium (Weir 1972; Holdo, Dudley & Mcdowell 2002; Chamaillé-Jammes, Fritz & Holdo 2007).

2.3 The importance of elephant sociality and cognition on resource use

Density dependent population regulation is most likely to result from higher calf mortality during droughts (Conybeare & Haynes 1984; Loveridge et al. 2006; Moss & Lee 2011), although older elephants can also suffer higher mortality during droughts (Dudley & Criag 2001). Social dynamics within and between elephant family group play a central role in calf survival (Moss & Lee 2011). Large variability in elephant group size from a few individuals to aggregations of several hundred individuals reflect the fission-fusion dynamics of nested societies (Wittemyer, Douglas-Hamilton & Getz 2005). The basic social unit is the mother-calf unit, the following level are families that are stable groups of about 10 individuals composed of closely related breeding females and their offspring led by a matriarch. Larger aggregations such as bond groups or even more loosely related clans may appear during the rainy season but break apart during the dry season when resources become scarce (Wittemyer, Douglas-Hamilton & Getz 2005). Studies in Northern Kenya revealed dominant family groups remain within the protected areas during the dry season whereas subordinate groups move out of the reserve (Paper *et al.* 2007). Subordinate individuals were exposed to higher risk outside of protected areas, their movement patterns followed multiday cycles suggesting intermittent access to water whereas dominant groups that stayed in the reserve had diurnal cycles suggesting much more regular access to resources and lower energy expenditures (Wittemyer et al. 2008). Each family group's social rank and experience, which are largely determined by the age of the matriarch, explain substantial variability in resource use amongst different family groups.

3 The trip: the right scale to investigate resource use

Movement ecology relies on the correlation between an individual's location(s) and the attributes of the given location(s) to infer processes relevant to the individual's life history or the functioning of its environment. Locational attributes can reflect environmental conditions such as resource abundance (van Beest et al. 2010; Martin et al. 2015), predation risk (Hebblewhite & Merrill 2009; Courbin et al. 2015) or even temperature (Kinahan, Pimm & van Aarde 2007; van Beest, Van Moorter & Milner 2012). Locational attributes can also be obtained directly from movement patterns such as speed and turning angles (Jonsen, Flemming & Myers 2005), residence time or recursions (Benhamou & Riotte-Lambert 2012) or changing directions (Byrne *et al.* 2009; Polansky, Kilian & Wittemyer 2015). However, these correlations only enable us to make an inference that needs to be validated. Accurately identifying foraging bouts and mapping them provides information about foraging behaviour such as distance between patches, patch residence time, patch size (Brooks & Harris 2008). Yet, few studies confirm these inferences in the field (but see Macandza, Owen-Smith & Cain 2012a).

Analyses of movement patterns as a function of scale can generally be categorized as bottom-up or top-down approaches. Bottom-up approaches are based on the identification of behavioural states that can be associated with specific resource use (i.e. immobility for resting, reduced speed and tortuous paths in a foraging patch or greater speed and directional movement during directed movement between patches). The identification of such behavioural states can be based on statistical models such as state space models (Jonsen, Flemming & Myers 2005), residence time (Barraquand & Benhamou 2008). Alternatively, behavioural states can be inferred from previous knowledge of the species' activity patterns and behaviour such as the time when foraging intensity peaks (Owen-Smith & Martin 2015). Top-down approaches consist in the identification of stationary phases in the movement pattern (Cornélis et al. 2011; Benhamou 2013) to define the extent of the investigation. The properties of the stationary home-range and spatial use within the home-range can then be investigated.

In the case of multiple central place foragers like elephants, the scale of interest is intermediate. Identifying visits to waterholes reveals elephant movement patterns during the dry season are highly structured and periodic (Chamaillé-Jammes et al. 2013). Although periodicity in animal movement has been identified without formally identifying the recursion site (Wittemyer et al. 2008; Polansky, Douglas-Hamilton & Wittemyer 2013), the distinction between different trips and their categorization can directly be interpreted in terms of resource use strategies (Chamaillé-Jammes et al. 2013). Following studies that explicitly acknowledge the constraints on animal movement imposed by central or multiple central foraging (Matthiopoulos 2003), we chose to use the trip framework identified by Chamaillé-Jammes et al. (2013) (Figure 4) to explore the seasonal changes in drinking and foraging patterns (chapter 2) and in habitat selection during foraging (chapter 3). Central place effects

were no longer at the core of our investigation in chapter 4, we used a more classical approach that consisted in basing our habitat selection analyses on foraging bouts defined a priori by the species activity patterns (Owen-Smith & Martin 2015).

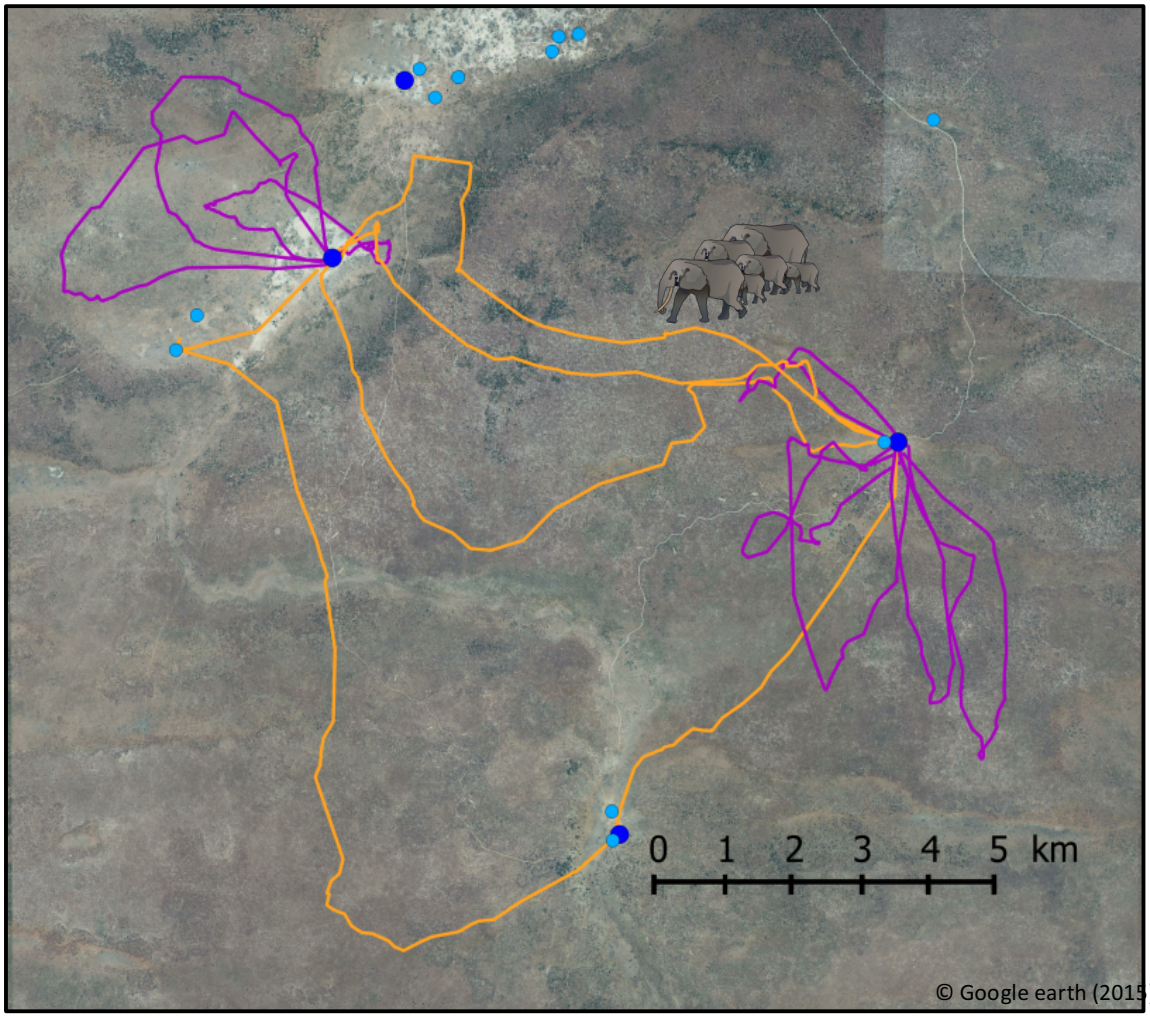


Figure 4: Elephant trips between waterholes. During looping trips (purple) elephants return to the same waterhole whereas during commuting trips (orange) they travel to a different waterhole. Permanent pumped waterholes are shown in dark blue, smaller natural pans in light blue

4 Thesis outline

The aim of this thesis is to understand the individual movement strategies of elephants confronted with seasonal fluctuations of two key resources: water and forage. The first step was to quantify these seasonal fluctuations and accurately map and describe the dynamics of seasonal water pans in Hwange National Park. These dynamics are put into perspective with the large scale elephant movement patterns on chapter 1 as a framework for the following three chapters. Chapters 2, 3 & 4 are draft manuscripts to be submitted to peer-reviewed journals, they were reformatted for the purpose of this thesis.

In chapter 2, I use the central place foraging framework to analyse elephant response to the intensification of the water vs. forage trade-off throughout the course of the dry season. The chapter includes two appendices that can be read independently. Appendix 1 describes the methodology that was used to accurately define visits to waterholes and segment the trajectory into trips. Appendix 2 explores the relationship between drinking time and trip duration.

In chapter 3, I shift the focus from central place effects to the landscape effects of water distribution on elephant habitat selection during foraging trips. The chapter discusses the implications of multiple central place foraging and landscape complementation on resource depletion by elephants.

In chapter 4, I extend the scope of the study to the effects of surface water availability on interspecific interactions throughout a yearly cycle. To do so, I compare the habitat selection patterns of elephant bulls and an African buffalo herd according to areas used by cattle that made incursions into Sikumi Forest, a protected area on the North-East boundary of Hwange National Park.

To conclude, the relevance of these findings to foraging theory and landscape ecology are discussed as well as the management implications in a context of aridification due to climate change.

Chapter 1: Even the rain
Rainfall, seasonality, game water supply and elephant movement in the Hwange ecosystem.

Figure 5: First rainbow, Ngweshla pan, Hwange National Park November 11th 2013

Introduction

To understand the drivers of resource use by elephant it is necessary to take into consideration the intrinsic spatiotemporal scales that characterize the distribution in time and space of these resources. The aim of this chapter is to describe the relevant scales at which variations in surface water availability and forage affect elephant movement in the Hwange ecosystem.

Hwange National Park extends over nearly 15 000 km^2 of woodland savanna on the north-western border of Zimbabwe. (18°29'S to 19°53'S 25°47'E to 27°28'E, Figure 6), 80 km to the south of Victoria Falls and the Zambezi river. Only three seasonal rivers (the Deka, Lukosi and Inyantue) drain the north of the park and the Nata River runs along the southernmost tip of the park. The closest perrenial river is the Gwayi, which flows to the North-East; 15 km to 20 km from railway line that delimits the eastern boundary of the park.

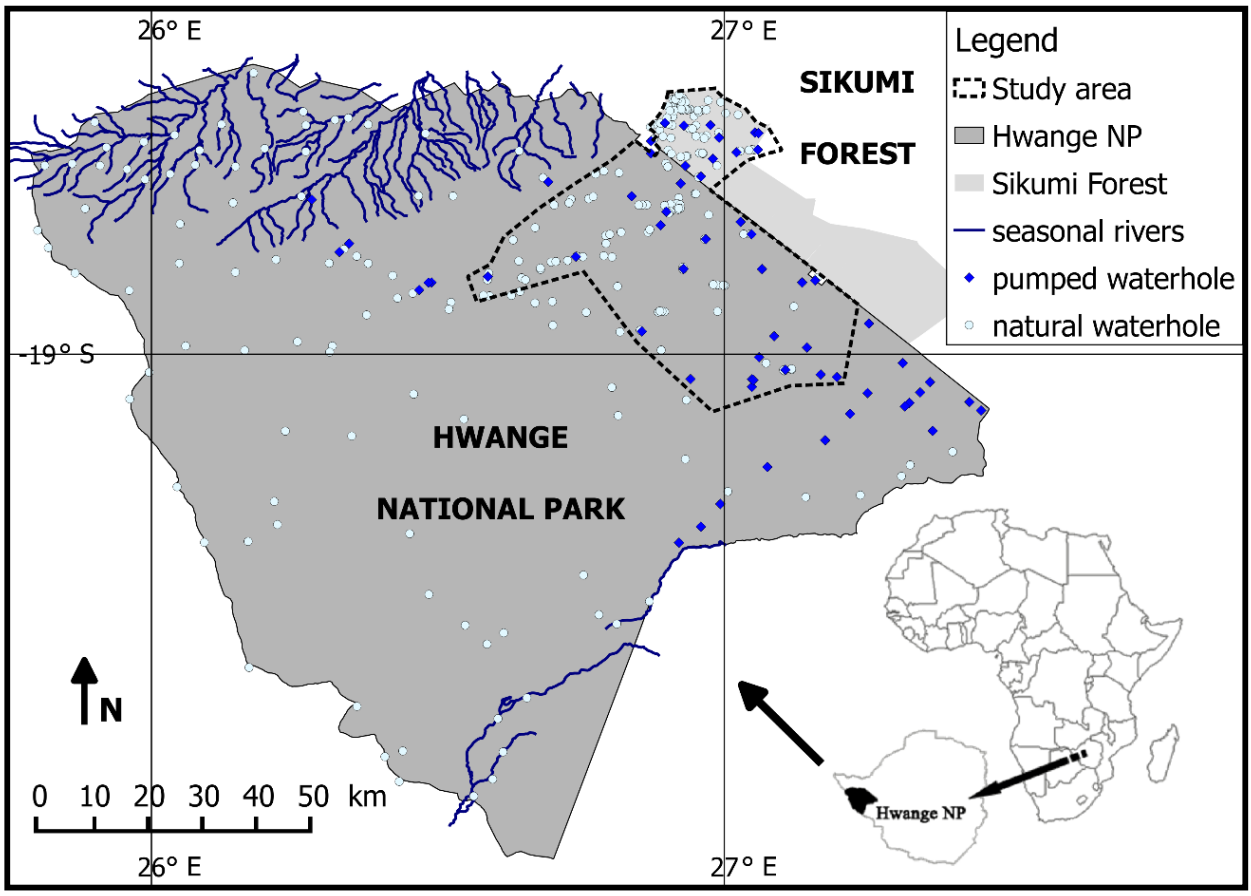


Figure 6: Distribution of major water sources in Hwange National Park and Sikumi Forest. Surface water availability was monitored in the 2000 km2 study area in 2013 and 2014.

Located on a continental divide, with altitudes ranging from 1000 to 1100 m above sea level, two thirds of Hwange consist in a relatively featureless (and riverless) plateau covered by aeolian Kalahari sands which may reach up to 60m in depth (Conybeare 1991). Mean annual

precipitation is c. 600mm, with large variations between years (Chamaille-Jammes, Fritz & Murindagomo 2006). At least 80% of rainfall occurs during the rainy season between November and April (Figure 7).

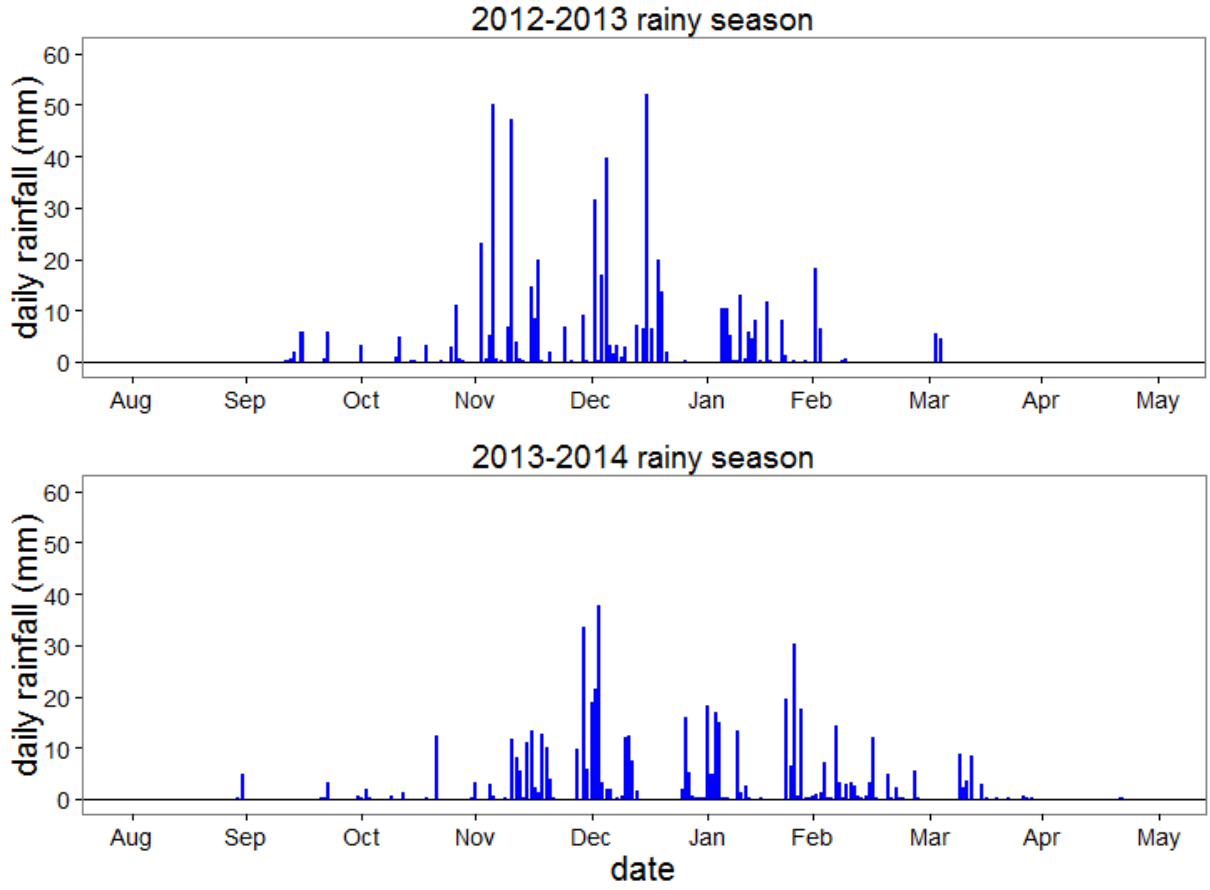


Figure 7: Daily rainfall recorded in Main Camp , Hwange National Park, obtained from the Hwange LTER-CNRS weather station for two consecutive seasons: 2012-2013 (top panel) and (2013-2014) bottom panel.

Hwange alternates between times of abundance and times of scarcity. During the rainy season, forage is plentiful and tens of thousands of shallow depressions, also known as pans, fill with water throughout the park (Figure 8). During the dry season, the vegetation withers and remains dormant while the pans gradually dry up until the park becomes virtually devoid of natural water sources (Figure 8). During years with above average rainfall, some of the larger pans may retain water throughout the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007b). In other years, natural pans may dry up months before the first rains. At the end of the dry season, wildlife exclusively relies on water pans artificially maintained by pumps extracting water from aquifers through boreholes up to 100 m deep. As a result of water scarcity in the dry season, providing reliable drinking water for wildlife (also known as game water supply) has been the main preoccupation of Hwange NP managers ever since the first warden's earliest report (Davison 1930), up to this day.

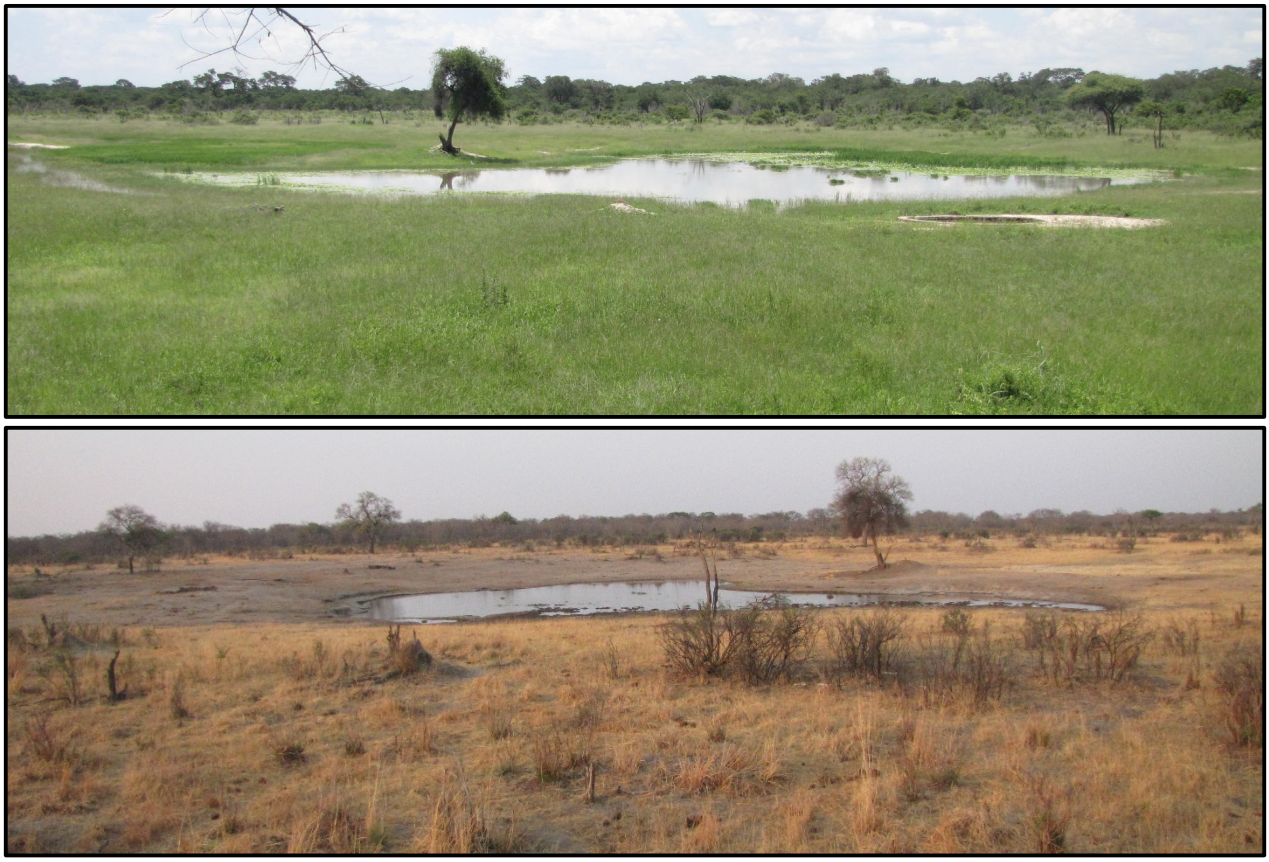


Figure 8: Livingi, a pumped water pan, during the rainy season (29/01/2013) and at the end of the dry season (15/10/2012).

The creation of artificial water sources is a widespread practice enabling the sedentarisation of herbivores during the dry season (Davison 1967; Western 1975; Leggett 2006a). Historically, elephants would not remain in the Hwange area during the dry season and presumably migrated to perennial rivers beyond the park's boundary (Davison 1967). The first borehole was sunk and equipped with a windmill in 1936. As early as the 1940's, windmills were supplemented and eventually replaced by diesel pumps that provided a more reliable supply with 6 artificial water pans in Hwange during the 1940's (Davison 1967). From the 1940's onwards one or two new boreholes were sunk every year to accommodate the increasing herbivore population (Davison 1967). Ultimately the number of active boreholes peaked around 60 by the 1990's (Owen-Smith 1996).

As early as the 1940's, "the permanency of water supplies soon began to have its effect on game migration" (Davison 1967). In a recent study concomitant with the addition of two artificial water supplies in north-western Namibia, Leggett (2006) reports the additional water supplies elicited substantial and rapid changes in elephant distribution and behaviour. Artificial water points allowed breeding herds to expand their range to areas that were previously beyond their reach, and even led to the sedentarisation of a group in the vicinity of the new resource. Elephants may also changes their foraging patterns by feeding closer to water and increase their drinking frequency. At the scale of Hwange National Park, artificial

water supplies created a novel ecosystem (Hobbs, Higgs & Harris 2009) characterized by unprecedented perennial water availability during the dry season that supports high elephant densities (Chamaillé-Jammes et al. 2008; Fritz et al. 2011) and their cascading effects on other species (Valeix, Chamaillé-Jammes & Fritz 2007; Valeix *et al.* 2011).

The following description gives a brief overview of changing environmental conditions and elephant movement patterns throughout a yearly cycle during the first decade of the 21st century. Our description of the yearly cycle focuses on two transitions: The first is a major discontinuity triggered by the onset of the rainy season between October and December. It is followed by a brief stationary phase, the rainy season, which generally lasts until March or April. The second transition is the dry season which is characterized by the decrease in resource availability until the rains return.

The onset of the rains and of the partial elephant migration

Seasonal rainfall results from the southward movement of the Inter-Tropical Convergence zone (ITCZ) during the austral summer. Precipitation events occur when large cloud formations known as Tropical Temperate Troughs (TTT) shift southward during the austral summer under the influence seasonal tropical convection variation and transient perturbations. The location of the TTT over Southern Africa may vary resulting in strong intra-seasonal and inter-annual rainfall variability (Usman & Reason 2004; Macron et al. 2014). TTT rain producing events typically last 3 to 4 days and consecutive events are separated by about 5 days (Usman & Reason 2004). Rainfall events are particularly erratic during the onset of the dry season between October and December (Figure 7). Sporadic showers with less than 30mm precipitation are not sufficient to fill the water pans for more than a couple of days (pers. observation). However once the threshold has been surpassed, the interval until the next rainfall event is generally short enough for pans to keep water until the next dry season.

Vegetation in Hwange responds to precipitation with a delay of about 1 month (Chamaille-Jammes, Fritz & Murindagomo 2006). As a result, the spatiotemporal heterogeneity of both rainfall patterns and vegetation green-up can be captured by variations in NDVI. Using a 10 year (9 rainy seasons) time series the start of the rainy season was estimated by the TIMESAT computer program (Jönsson & Eklundh 2004). On average, Hwange National Park greens-up within a couple of weeks following the first larger downpours (Figure 7) around the beginning of the month of November (Figure 9). The onset of the rainy season appears to be unpredictable in time and space. Vegetation green-up can vary by a few weeks up to a month between different parts of the park for a given year and between years for any given area (Figure 9).

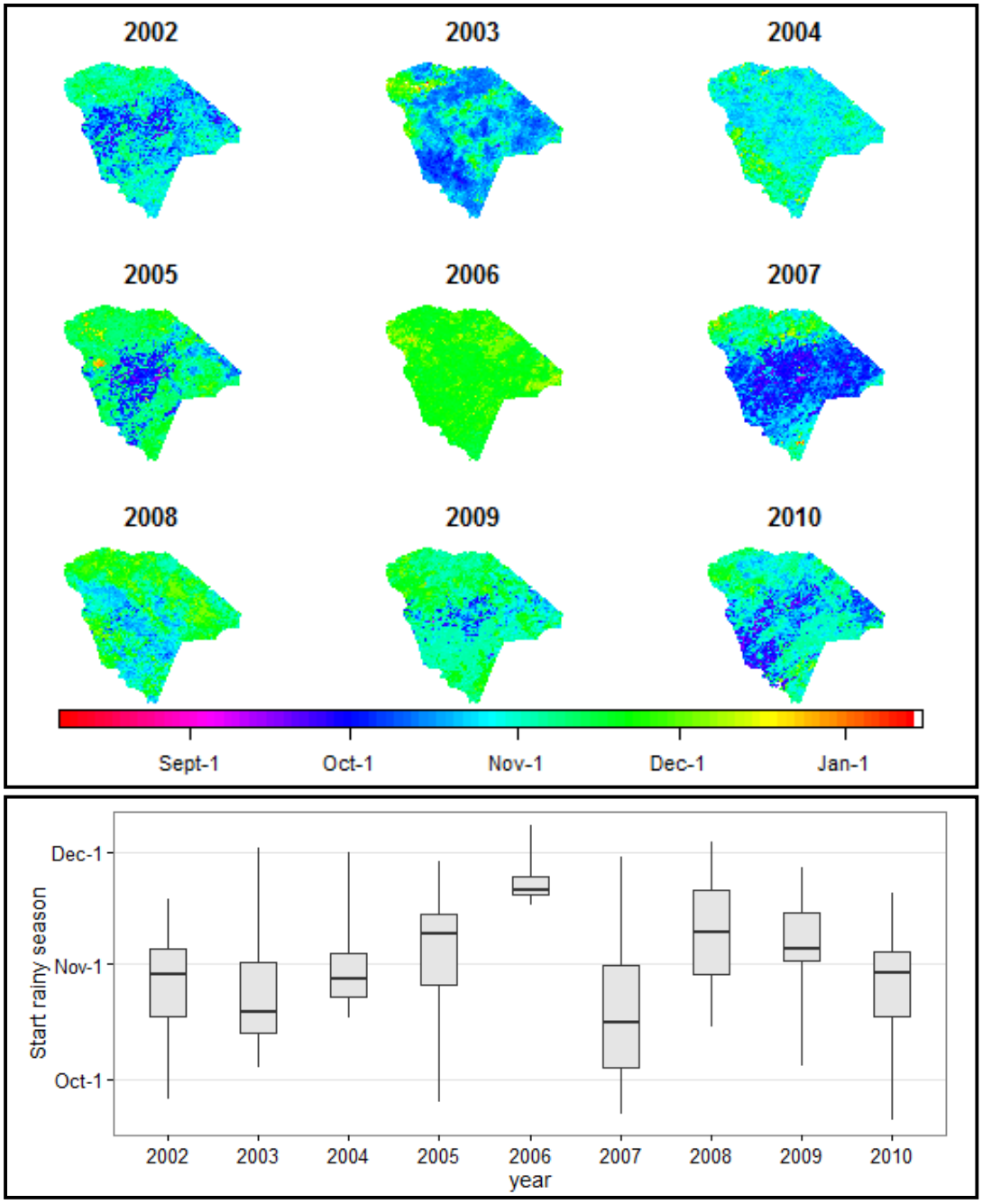


Figure 9: Variability of the start of the rainy season between 2002 and 2010 for Hwange NP. The top panel shows the spatial variability of the onset of the rainy season from an early start (purple-blue) to a late start (green-yellow). The bottom panel summarizes the range of these starting dates.

The NDVI, patterns reveal one of the aspects of the 2005-2006 drought, which was the absence of the heterogeneous rainfall events at the beginning of the 2006-2007 rainy season which resulted in a delayed yet homogenous green-up when the rains finally arrived.

It has long been known that Hwange elephants migrate South-West during the rainy season and return to the Northern and Eastern parts of the park during the dry season, since permanent water supplies have been made available (Davison 1967; Conybeare 1991). Out of 13 adult females belonging to different family groups, collared in October and November 2012, 5 were long distance migrants, 5 were short distance migrants and 3 were residents (Figure 10). However, these numbers cannot be taken at face value. Collared elephants represent about 1% of the estimated population; an accurate estimation of the number of migrants is still pending.

The seasonal home-ranges of long distance migrants do not overlap, they travel between 100 and 200 km from their dry season range, beyond the international border with Botswana (Figure 10). The seasonal home-ranges of short-distance partially overlap (Figure 10). Short distance migrants typically shift their home-ranges by 20km - 60km away from areas around water pans used during the dry season. The seasonal home-ranges of resident elephants remain largely unchanged (Figure 10).

Elephant migratory patterns can be seen as successions of transitory relocations and stationary phases during which elephants remained within a small area for several days, weeks or even months (Benhamou 2013). Despite the shared large scale North-West to South-East movement; the extent, timing and duration of the transitory and stationary phases as well as the resulting migratory pattern were highly idiosyncratic yet surprisingly similar between years (Figure 10**Error! Reference source not found.**). Hwange migratory patterns suggest a two-step response to rainfall by elephants. Elephants initially become increasingly mobile as soon as the first showers occur (Garstang et al. 2014). Areas having received the first rainfall will also be the first to green up and may be subsequently selected by elephants (Wall *et al.* 2013; Bohrer *et al.* 2014).

However, the migratory-resident distinction is associated with differing small scale movement patterns. During the hot-dry to rainy season transition, all elephants increase their total daily displacement (Figure 11) and make transient trips outside of their dry season home-range. For long distance migrants, daily displacement increases on average to 15km-20km a day, whereas daily displacement only increases to 15km a day for short-distance migrants and remains close to 10km for residents. These heterogeneous movement patterns are similar to phases of restless behaviour described in numerous migratory species (Bauer et al. 2011). The transient trips occur immediately after rainfall events (pers. observation), when conditions are favourable migrants will continue until they reach their rainy season home-range, otherwise they return to their dry season home-range until the next precipitation event (Figure 10).

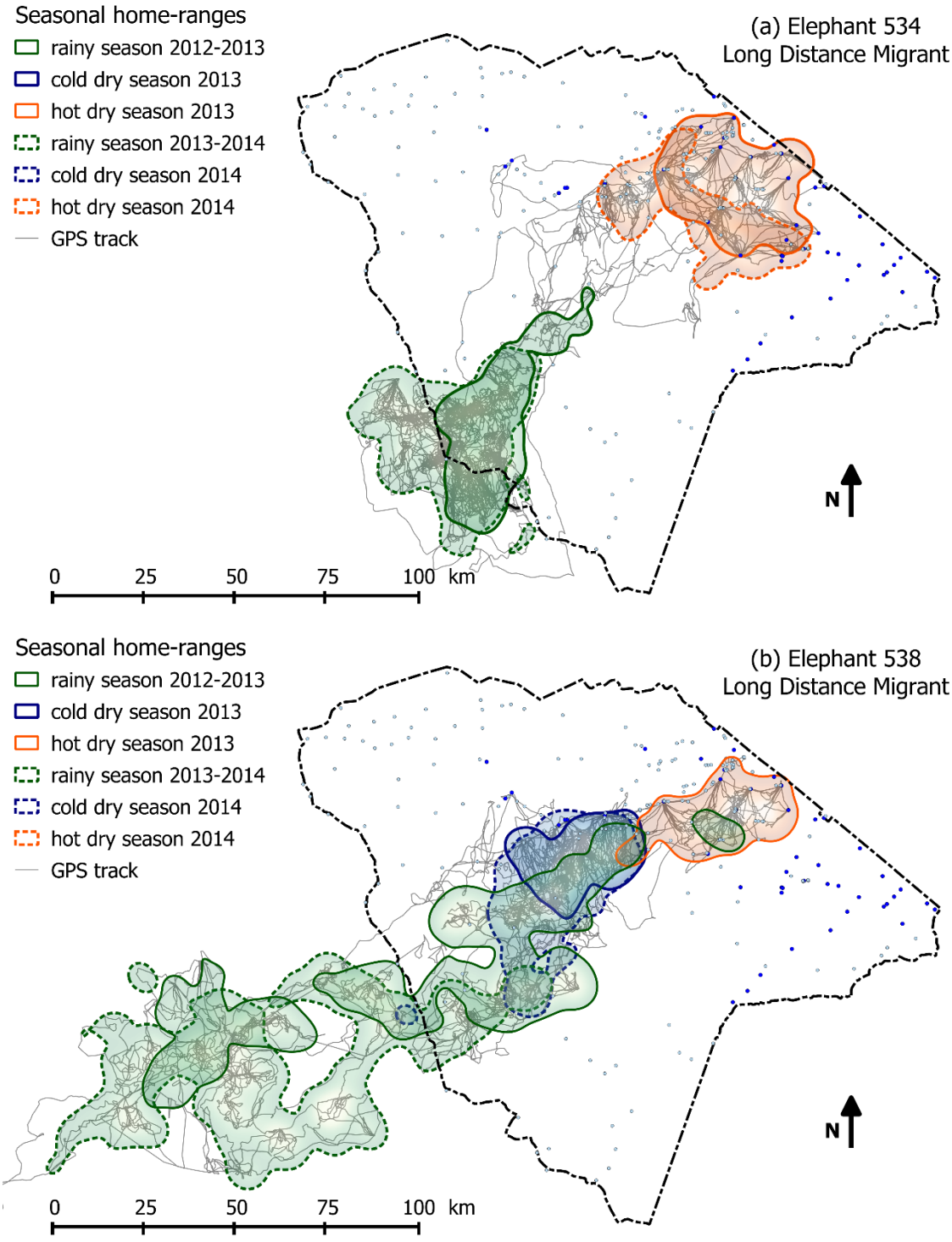


Figure 10: Seasonal home-ranges of female elephants over a two year period. Long distance migrants can either travel for a couple of weeks to their rainy season home-range each year (a) or adopt a nomadic ranging pattern during the rainy season before settling during the cold dry season (b).

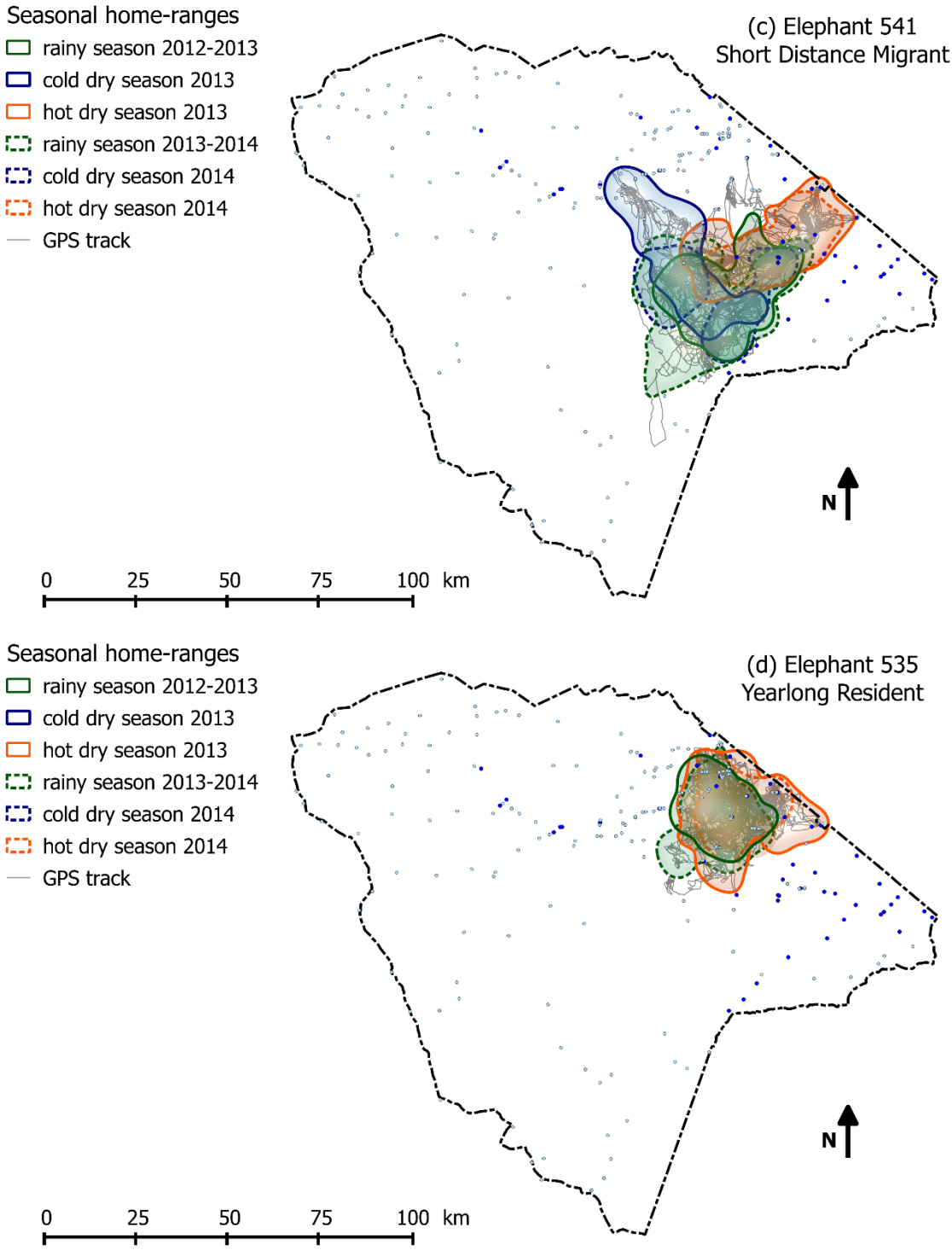


Figure 10 (continued): Seasonal home-ranges of female elephants over a two year period. The seasonal home-ranges of short distance migrants partially overlap (c) whereas the home-ranges of resident individuals slightly contract during the rainy season (d).

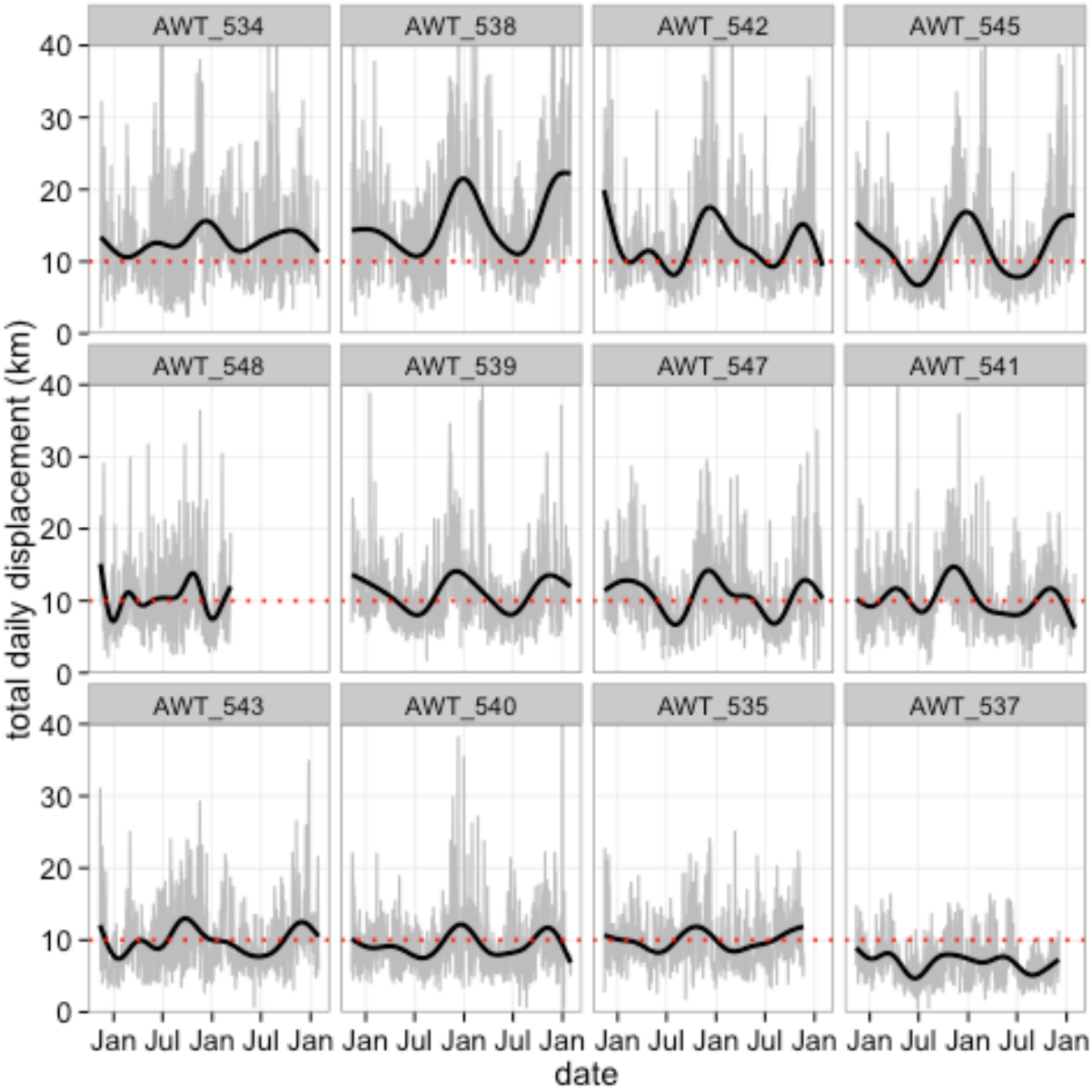


Figure 11: Total daily displacement (30min fix rate) of 12 collared elephants. Mean daily displacement and the amplitude of oscillations were greater in migrants: Long distance migrants (top), short distance migrants (middle) and residents (bottom).

The dry season: reassertion of water dependency

After the rains gradually come to an end between the months of March and May (Figure 7), temperature changes substantially during the dry season (Figure 12). Three seasons can be identified on the basis of Temperature variations. The rainy season (green) is characterized by high mean temperature and small daily fluctuations (mean $_{February}$ =23±5°C). The cold dry season (blue) is defined by decreasing temperatures and increasing daily fluctuations (mean $_{July}$=13±10°C) and the hot dry season (yellow) is defined by increasing temperatures and large daily variations (mean $_{October}$ =24±10°C). As a result, evaporation decreases during the

cold dry season. During the hot dry season, the combination of higher temperatures (Kinahan, Pimm & van Aarde 2007), dryer vegetation and fewer water pans increases elephant's water dependency (Chapter 2).

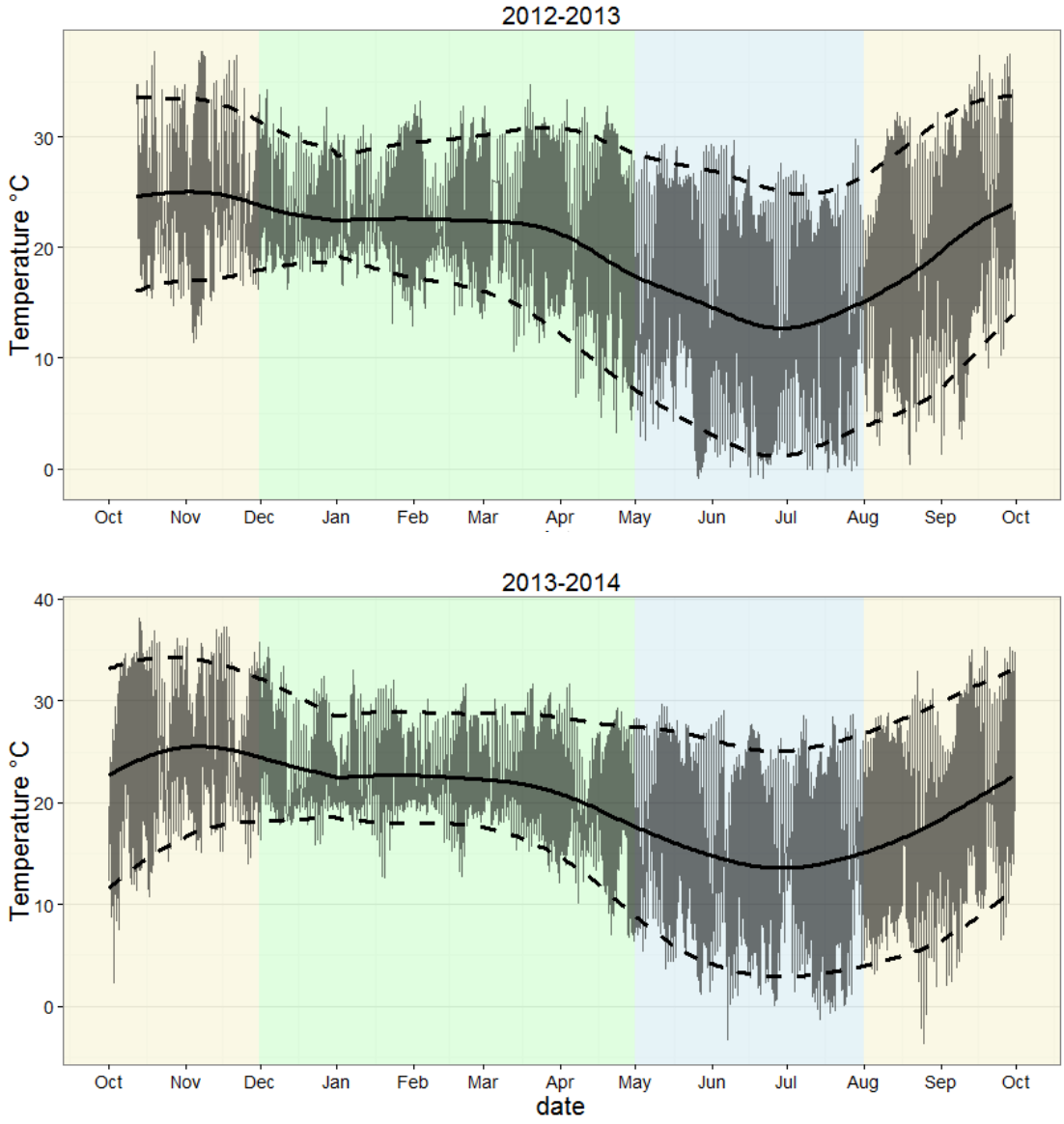


Figure 12: Hourly temperatures variation in Hwange National Park , Main Camp, obtained from the Hwange LTER-CNRS weather station for two consecutive seasons: 2012-2013 (top panel) and (2013-2014) bottom panel. Seasonal trends are given by Generalized Additive Models (GAM) calculated for mean daily temperature (full line), minimum and maximum daily temperatures (dashed lines).

Water pans in Hwange NP are shallow depressions ranging from a few dozen to a few hundred meters wide at their fullest, during the rainy season. Pans are kept watertight by a thin layer of compact clay (Davison 1967). The size of water pans reflects the surface area of the depression with this clay lining. The surface area of natural pans was measured by walking around the shoreline with a handheld GPS (Garmin GPSMAP 64s). The track was then

converted to a polygon with (Quantum GIS v2.4) to calculate the surface area. Pans were visited roughly on a monthly basis until they dried out completely. Pan sizes were surveyed in Hwange NP in 2012 and 2013. In Sikumi Forest a systematic survey was conducted on foot as soon as the rainy season ended. The survey included many small pans that dried up within the first month after the rains in March and April. Pans were visited regularly to estimate dry-up date in 2014, but surface areas were no longer measured.

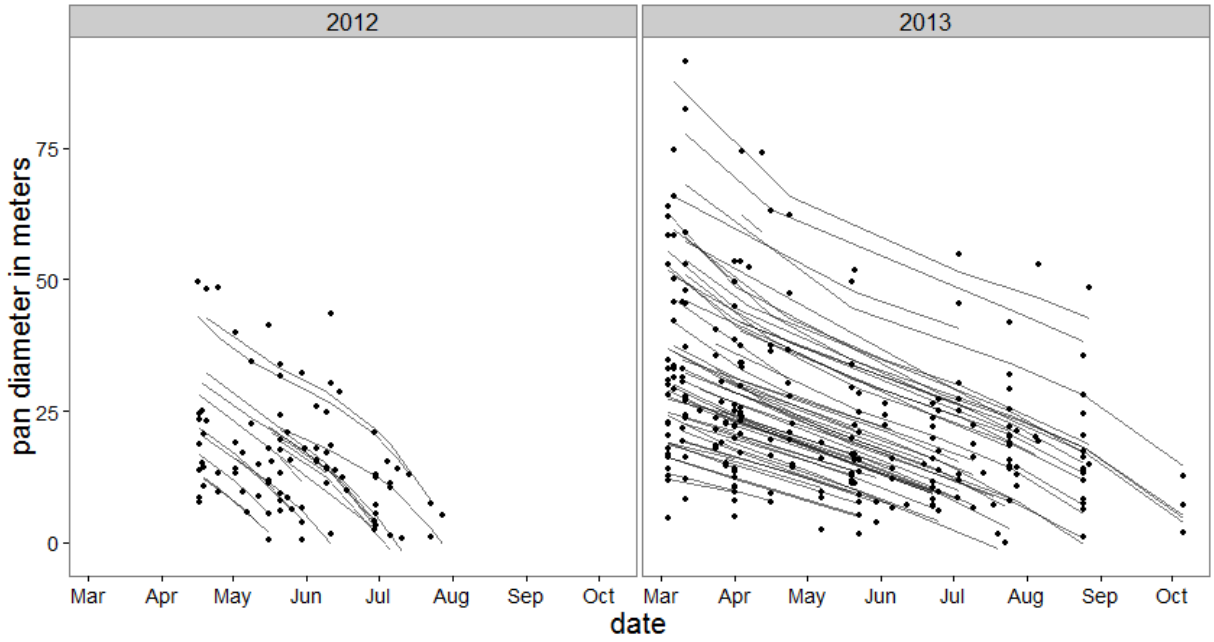


Figure 13: Natural water pan dry-up. during a year with below average rainfall (2012) and a year with average rainfall (2013). Lines represent individual pan trajectory estimated by linear mixed model including dry-up date and time of the year as fixed effects and pan id as a random intercept

The main factor determining pan longevity is total yearly precipitation and pan size (Figure 13). All water pans dried up earlier and faster in 2012 (below average rainfall) than in 2013 (average rainfall: 568 mm at Main Camp). At any given time pan size was a better predictor of pan longevity than the time of the year although the longer time-series in 2013 suggests evaporation rates are greater when temperatures are higher before April and after August than during the cold dry season (May-June). Finally, the dry-up seems to accelerate when pan size reaches a minimum threshold (10-20m diameter) regardless of the time of the year. The difference between the rates of dry up between both years may be the direct effect of drinking by larger numbers of herbivores at fewer pans, particularly elephants that consume more than 100L a day per capita.

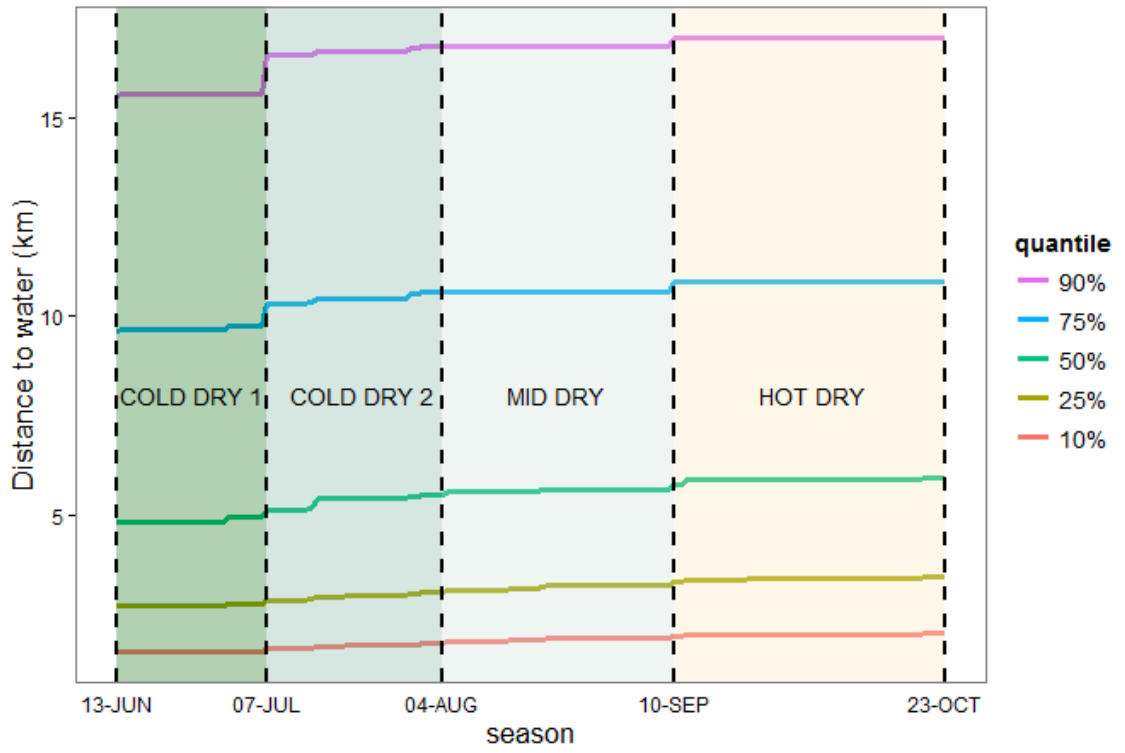


Figure 14: Gradually increasing distance to water within the combined dry season home-range of collared elephants in 2013. The cuttof dates correspond to the return time of elephants from their migration and the first transient movements following a large storm at the center of the park on October 23rd.

On the basis of this survey we estimated surface water availability throughout the study area during the dry season. In Hwange National Park, many smaller pans along the drainage lines were too far from roads to be monitored (Figure 6). However, an aerial survey in April 2013 gave us a baseline of pan locations and sizes. Since, we had identified pan size was a good indicator of dry up, surface water availability was only estimated once similar sized pans we were monitoring had dried up at the beginning of the month of June 2013.The effects of inter-annual and seasonal variability on surface water availability is largely buffered by the artificial water supply (Chamaillé-Jammes, Fritz & Murindagomo 2007b). Due to the regular spacing of pumped water pans, distance to water in the elephant's dry season home-range does not increase as much as the rate of pan dry-up would suggest (Figure 14). However, the buffering effect of pumping was limited by chronic breakdowns and fuel shortages. A survey of pumping effort revealed some pumps were out of use up to half of the time during the dry season. The consequences of such interruptions largely depended on the type of pan. Larger pans could withstand several days without pumping; however the smaller pans and particularly pans lacking the clay seal would dry off within 24h of a breakdown.

Towards March, when the rains come to an end, migratory elephants generally settle into smaller seasonal ranges as their movement rate decreases. The seasonal range may be part of their early rainy season range (Figure 10a) or be a distinct cold dry season home-range located between the rainy season and hot dry season home-ranges (Figure 10b,c). Elephants appear to remain in these ranges until their water supply runs out. Thus the timing of the return migration fluctuates widely between years. For instance, Elephant 534 returned on July 2nd in 2013 and August 25th in 2014. In years with more widespread water availability individuals may not return to their hot dry season altogether (e.g. Elephant 538 in 2014 Figure 10b).

Throughout the dry season, elephants in Hwange remain within 15km of water (Conybeare 1991). As the dry season progresses, elephants spend less time close to and far away from water. Elephants' use of areas beyond 5km from water increases during the cold dry season then decreases during the mid and hot dry seasons (Figure 15). Throughout the dry season, elephants spend less and less time close to water, as shown by the boxplots in Figure 15.

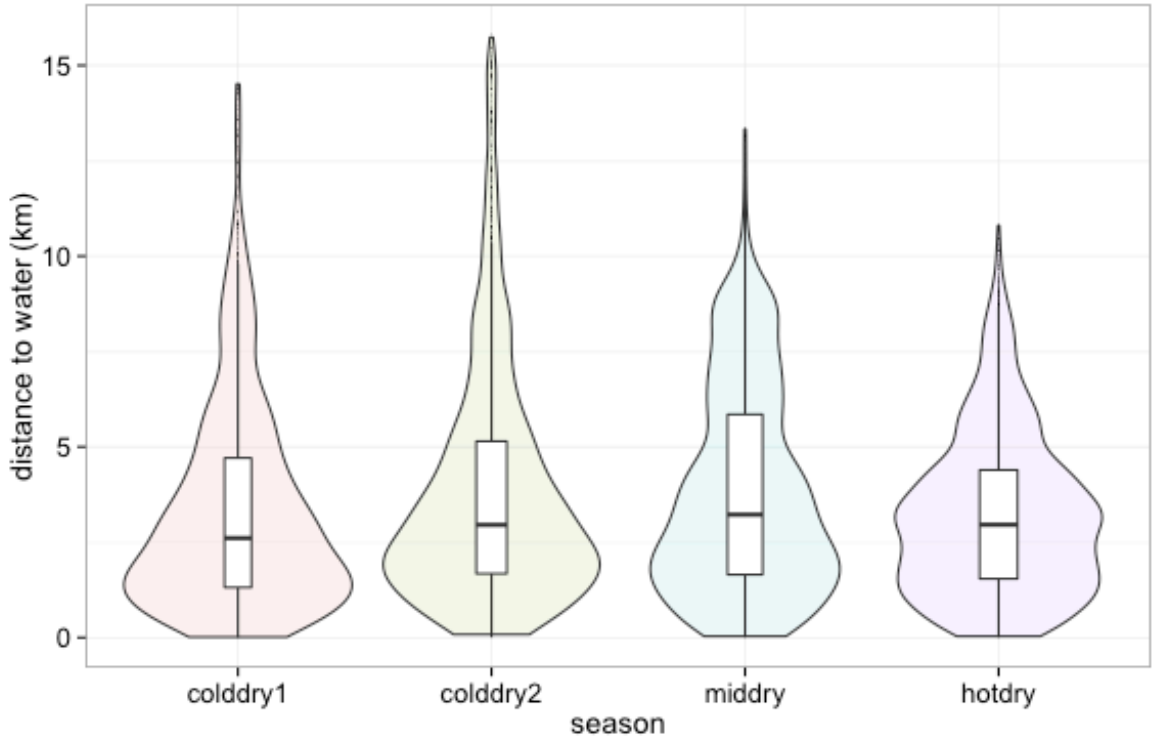


Figure 15: Distribution of elephant utilization according to distance to water by season. Boxes range from the 25th to 75th percentile, including the median (horizontal black line).

Conclusion

The scale of an investigation is characterized by both its extent (the study area and the study period) and its grain (the spatial and temporal resolution of observations) (Wiens 1989)The extent of this study is defined by the behaviour of migratory collared elephants: The spatial extent was given by the dry season home-ranges over which surface water availability dynamics could be quantified. The temporal extent was restricted to the stationary phase associated with dry season home-range occupancy starting after the last migrants had returned and ending before the transition towards the rainy season triggered by the first rains. The grain of environmental variables was given by the rate of water pan dry-up during the dry season. The grain of movement patterns was constrained by GPS collar sampling frequency which was sufficient to accurately define visits to waterholes and foraging trips (chapter 2).

Unfortunately, migration of most of the collared individuals implied that they used areas that were too remote to collect field data on their rainy season home-range. This precluded comparisons of space use and habitat selection with periods when elephants were not constrained by drinking water during the rainy season. We focused our study on the dry season during which the continuous knowledge of surface water distribution provided a template for the segmentation of elephant movement paths into trips during the dry season by correctly identifying visits to waterholes (chapter 2). Distance to water (chapter 2) and waterhole density (chapter3) were then used to investigate the mechanisms by which elephants solved the trade-off between drinking and foraging as temperatures increase during the dry season (chapter 2) and acquire a better understanding of their habitat selection criteria (chapter 3). In order to extend the scope of the study to the rainy season, the spatial extent was reduced to a smaller study area (Sikumi Forest) within which the spatial distribution of surface water during the rainy season could be accounted for (chapter 4).

Chapter 2: The need for speed
Do African elephants mitigate travel time constraints as the dry season progresses?

Hugo Valls Fox, Hervé Fritz, Michel de Garine-Wichatitsky, Simon Chamaillé-Jammes.

Abstract

- Sparse distribution of water in arid landscapes produces central place effects whereby animals will regularly visit waterholes to drink between foraging trips. As the dry season advances, foraging resources close to water become depleted and water requirements increase due to elevated temperatures. Animals must balance their need to travel far to meet their feeding requirements and returning to water often to avoid dehydration.

- Few studies have investigated how an individual can use its navigational and locomotional capacities to overcome this kind of trade-off. We studied travel choices (distance, speed, straightness) of 8 collared female African elephants, during the course of the 2013 dry season, in Hwange National Park, Zimbabwe.

- From the onset of the dry season elephants maximize their foraging time away from water by travelling faster when close to water and by making directed movements away from water pans.

- However, as the dry season advances elephants visit waterholes more often and travel further during 24h trips. They manage the trade-off by increasing their travelling speed at the beginning and the end of these trips. Elephants are able to maintain the number of 48h trips but not the longer 72h trips that disappear at the end of the dry season.

- We show elephants can use their locomotional and navigational faculties to solve central place foraging trade-offs. Our study suggests that during the dry season the short term costs of thermoregulation are more important for elephants than their long term nutritional needs. These currencies need to be explicitly incorporated in future foraging models to understand how one might mitigate the effect of drought on large herbivorous mammals.

1 Introduction

Changing resource abundance in time and in space is one of greatest challenges organisms have to cope with for their survival. Animals have developed the unique ability of moving over large distances to make the best of these fluctuations. Optimal foraging theory predicts an individual will seek a new foraging patch when the intake rate of a given patch drops to the mean rate of other patches (Charnov 1976). However some resources are non-substitutable and scattered in space. Individuals must therefore travel between these patches to fulfill their requirements. Rather than being limited by the mean quantity and quality of resource patches, animal populations are limited by each individual's ability to travel between these resources and successfully exploit them (Dunning, Danielson & Pulliam 1992). Therefore, from an individual's perspective the distance between non-substitutable patches underlies landscape quality. At larger scales, it is assumed animals will minimize travelling cost by selecting landscapes that provide optimal patch complementation. However, at smaller scales these distances may become irreducible and animals must visit non-substitutable resources patches within a given time in order to survive.

The functional response of non-substitutable resources often differ and generally lead to *central place effects* whereby one or a few patches of one resource will serve as a central place from which the individual travels to exploit the other resource. For instance, nesting and burrowing sites can be seen as a resource scattered in space. Parents select one of such sites and must then return to the central place regularly to feed their young (Mueller et al. 2009). Individuals must allocate time and energy to acquire each resource and travel between them. However time allocation is asymmetrical, for instance diving mammals and birds have adapted to limit breathing time while foraging underwater (Parkes *et al.* 2002; Hoskins, Costa & Arnould 2015) and large herbivores only spend a fraction of their time actually drinking at a waterhole (Valeix et al. 2008a; Rozen-Rechels et al. 2015). In the case of free ranging herbivores, these central place effects result from two processes: The long-term establishment of a piosphere (Lange 1969) and seasonal forage depletion. Piospheres change habitat availability along a distance to water gradient. They are generally characterized by reduced vegetation cover in proximity to water and changes in species composition due to herbivory (Thrash & Derry 2008; Chamaillé-Jammes, Fritz & Madzikanda 2009). Forage quality and quantity is expected to decrease faster closer to water due to exploitation competition (Birt et al. 1987; Shrader et al. 2012). In order to meet their feeding requirements free ranging herbivores make long foraging trips far away from water, particularly during the dry season for those living in arid or semi-arid environments. In Makgadikgadi and Nxai Pan National Park, Botswana, zebra (*Equus quagga*) travel on average 17.5 km from water and remain 4 days before returning to drink (Brooks & Harris 2008). Reports of Namib desert dwelling African elephants (*Loxodonta Africana*) indicate that they can travel 20-40km away from water for durations of up to 4 days (Viljoen 1989). However, in Hwange National Park, Zimbabwe, elephants remain within 15km of water (Conybeare 1991) while they periodically shuttle every

24h, 48h or 72h between their foraging grounds and waterholes (Chamaillé-Jammes et al. 2013). To respond to the constraint of fulfilling both their feeding and watering requirements large herbivores face a dilemma: should they travel afar and risk dehydration or remain close to water and risk starvation?

Herbivore may respond to this trade-off by modifying their foraging decisions in both time and space. African Buffalo (*Syncerus caffer*) limit their movement by shifting their home-ranges to suboptimal habitats in the vicinity of permanent water (Cornélis *et al.* 2011; Macandza, Owen-Smith & Cain III 2012; Bennitt, Bonyongo & Harris 2014). In a recent study Rozen-Rechels et al. (2015) showed that feral horses (*Equus ferus caballus*) selected for low quality patches close to water where densities were elevated and for high quality patches away from water where densities were low. They attributed the shift to depletion of the high quality patches found close to water. However, the terms of the trade-off changed in locations where horses dedicated more time to drinking, because they had to dig for water. The shift occurred closer to water suggesting they no longer had enough time to make longer foraging trips (Rozen-Rechels et al. 2015). Conversely, sable antelope travel further during the dry season, but additional travel comes at the cost of time allocated to foraging and resting (Cain, Owen-Smith & Macandza 2012). Few studies have investigated how an individual can use its navigational and locomotional capacities to overcome this trade-off. Hedenstrom & Alerstam (1995) and (Houston 2006) suggest that much could be learnt empirically by comparing travel speed of the same individuals as distance between patches varies. We answered this call and studied travel choices (distance, speed, straightness) of African elephants that continuously shuttle back and forth between waterholes and foraging patches as the dry season progresses.

To travel further without increasing trip duration one can only go faster or straighter. However, travelling faster is energetically costly. Birds will adjust their flight speed to maximize intake rate while foraging but minimize total energy expenditure while migrating (Hedenstrom & Alerstam 1995). African elephant is the largest terrestrial mammal with the lowest reported net cost of transport (Langman et al. 1995). This implies that unlike smaller animals it could be energetically worthwhile for elephants to increase travelling speed to reach remote high quality patches. During the dry season elephants spend on average 17-19 hours a day foraging (Moss, Croze & Lee 2011) but lose body condition and face higher risks of mortality (Conybeare & Haynes 1984) suggesting maintaining foraging time is key to their survival. In spite of their morphological and physiological adaptations, (Phillips & Heath 1992; Weissenböck et al. 2010) elephants need to drink regularly to maintain their body temperature (Rowe et al. 2013; Dunkin et al. 2013). We hypothesize elephants will increase travel speed if foraging gains outweigh both energetic and thermoregulatory costs.

Large herbivores have a propensity to travel in remarkably straight lines beyond their line of sight during directed movement (Brooks & Harris 2008). In the case of African elephants, a highly mobile species with recognized cognitive abilities, it is likely that they travel along straight lines throughout the study period to reach well-known resource patches such as

waterholes (Polansky, Kilian & Wittemyer 2015). Between two drinking events an elephant's foraging trip can be seen as a succession of straight directed travelling and more tortuous foraging bouts (Roever et al. 2014). At the scale of an entire foraging trip straightness can be seen as an indicator of foraging effort: When an elephant returns to the same waterhole it is expected to maximize trip straightness by making long directed outgoing and returning segments to forage far away from water. Conversely, when an elephant commutes between two different waterholes, trip straightness reflects its choice between foraging and drinking. Elephants are expected to travel straighter if their primary concern is to reach the next waterhole, whereas they should make a more tortuous journey off the beaten track when seeking better foraging opportunities.

Decreasing resource availability during the dry season provided us with an ideal template to study elephants' movement strategies in response to a strong trade-off between two non-substitutable resources: surface water and forage. We identified three spatio-temporal components of this trade-off: (i) as waterholes dry up, the absolute distance between waterholes increases, implying longer distances between waterholes. (ii) Concomitantly, elephants must travel further away from water to access better quality patches as foraging resources are depleted by increasing herbivore densities close to water (Valeix 2011). (iii) Finally, rising temperatures limit elephant locomotion (Rowe et al. 2013) and force them to return to drink and bathe more often (Dunkin et al. 2013).

2 Methods

2.1 Study site

The study was conducted in the eastern region of Hwange National Park, Zimbabwe (Figure 16). The area is characterized by relatively level terrain (alt. 1000-1100m asl) and the vegetation is typical of dystrophic semi-arid savanna. Mean annual precipitation is c. 600mm with large variations between years (Chamaille-Jammes, Fritz & Murindagomo 2006). The ecology of the Park is highly seasonal, about 80% of the annual rainfall occurs between November and April. Natural depressions and dams fill up with water during the rainy season but gradually dry up throughout the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007b). There are no perennial rivers in the Park, and at the end of the dry season surface water can only be found at artificial waterholes in which groundwater is continuously pumped. Water-dependent species such as elephants must undertake foraging trips to and from these waterholes (Chamaillé-Jammes et al. 2013). This creates local forage depletion near waterholes, and on the long-run habitat changes: vegetation cover increases with distance to water up to several kilometers away from these waterholes (Chamaillé-Jammes *et al.* 2009, unpublished information).

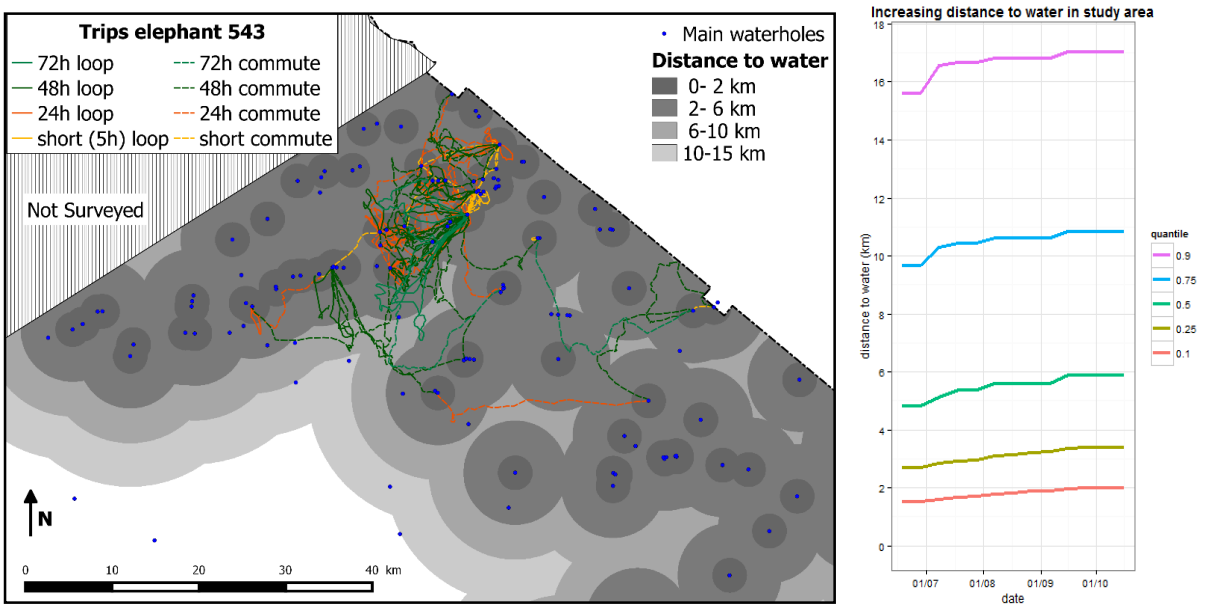


Figure 16: Water availability in Hwange NP during the dry season. (left panel). GPS tracks of one elephant breeding herd from June 13th to October 23rd 2013. Trips can be distinguished by their duration: short (yellow), 24h (orange), 48h (green) and 72h (blue) for both commuting trips (full lines) and looping trips (dashed lines). (right panel) Increasing distance to water of the study area defined as the union of each individual's 100% minimum convex polygon.

2.2 Data collection

The study was conducted during the course of the 2013 dry season. It rained 568 mm between November 2012 and April 2013. The study began on June 13th when the elephants had settled in their dry season home-range and ended on October 23rd when they dispersed again after the first significant storm. From April 2013 onwards we monitored all natural pans and artificial waterholes over a 2000 km^2 area (Figure 16). Movement data was obtained from thirteen adult females belonging to different family herds that had been equipped in November 2012 with GPS collars (Africa Wildlife Tracking). Collars were programmed to record a location every 30 minutes. Visits to waterholes were identified according to the method described in appendix 1. We retained data from 8 collars for which fix success rates enabled us to reliably identify visits to water. A trip was defined as elephant movement occurring between two consecutive visits to water. We identified 901 trips (appendix 1). We distinguished looping trips (62%) during which elephants returned to the same waterhole from commuting trips (38%) when elephants changed waterhole. Elephant trips are periodic: We identified 390 24h trips, 221 48h trips, as well as 50 72h trips and 240 short trips (mean=4.6h), the latter mostly occurred during the hot dry season (Figure 17).

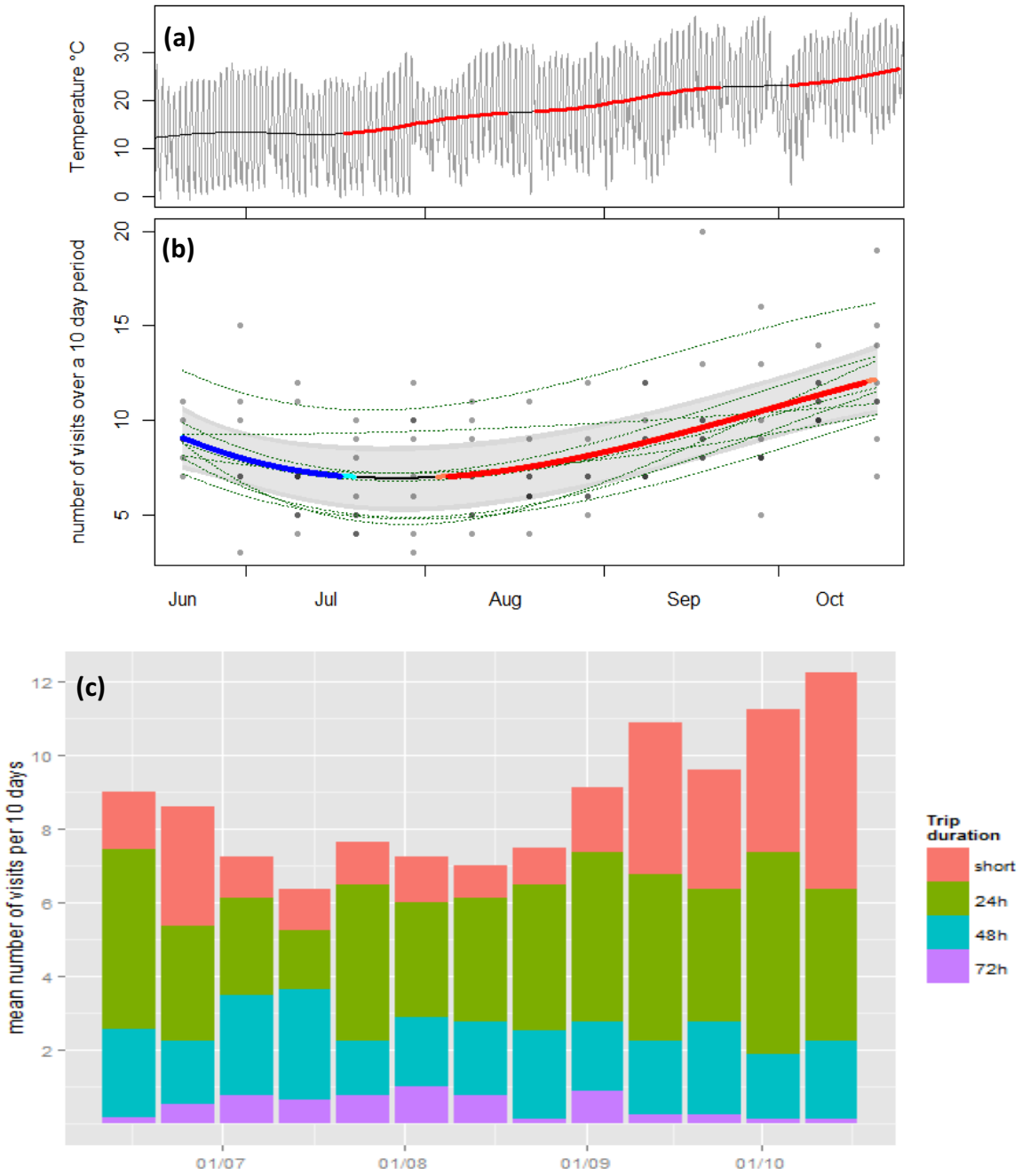


Figure 17: Visits to water according to ambient temperature. (a) Hourly ambient temperature at Main Camp weather station, Hwange NP. Significant mean temperature increases are shown overlaid in red. (b) Number of visits to water over successive 10 day periods by individual (data points). The main fixed effect (R2=0.26) is shown by the black curve with 95% confidence interval in grey. Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects (R2 = 0.69). (c) Average number of trips over successive 10 day periods. Note the sharp increase in short trips during the hot dry season mainly due to additional commuting trips.

2.3 Data analyses

We studied how drinking frequency (calculated over 10-day periods) (Figure 17) and trip characteristics changed during the course of the dry season. Various window durations were tested, a 10 day period appeared as the best compromise between shorter windows that were susceptible to the stochastic switch between long and short trips and larger windows that were too coarse to approximate a continuous change throughout the dry season Trip characteristics included trip duration (Figure 17) and maximum distance to both starting and finishing waterholes (Figure 18). For short trips we calculated mean speed (Figure 19) whereas for longer trips we calculated outgoing and returning speeds (Figure 20). The latter were averaged over 3h windows so as to describe speed while traveling to water (Polansky, Kilian & Wittemyer 2015) rather than a combination of foraging and travelling. The seasonal trends were qualitatively similar for 2h and 4h windows. Straightness (Figure 21) was defined as the ratio of the net displacement divided by total distance travelled (Valeix et al. 2010). We analyzed each class of trip separately because trip duration is highly multimodal (Appendix 2), in addition looping and commuting trips might serve different functions and affect elephant space use differently. In order to compare looping and commuting trips, net displacement was defined as the distance between both waterholes in the case of commuting trips and as twice the maximum distance to water for looping trips.

We investigated seasonal changes by fitting 3rd-order polynomial mixed models in which time was included as the only predictor. To account for intra-individual correlations random intercepts and slopes were included for each elephant identity. These models allowed us to plot seasonal curve for each response variable. As proposed by Simpson (Simpson 2014, see also Wood 2006), we obtained confidence intervals of the slope at each point of the seasonal curves using a Monte-Carlo approach. First, we generated 10 000 posterior simulations of the seasonal curve so that each simulation was consistent with the model fitted on the original data. Indeed, each generated curve was obtained by drawing new model coefficients randomly from a multivariate distribution (parameterized using the fixed effects and the variance-covariance matrix of the original model), and then recalculating new values of the response variable across the temporal axis. Secondly, for each generated curve we calculated the first derivative by differentiating the response variable across 1000 intervals (each interval thus represents 0.13 days). Confidence intervals (95% and 90% CI) on the derivatives were calculated by computing quantiles of the distribution of derivative values. When these intervals did not include zero this indicated that the response variable was displaying significant changes, and we identified these periods of change directly on the figures. Note that confidence intervals generally became larger at the beginning and at the end of the study period because of data scarcity. Therefore statistical significance was sometimes lost although rate of change may have remained unchanged.

3 Results

3.1 Drinking frequency

On average, elephants visit waterholes from one to three times within 48h. In order to drink more often, elephants shift to trips with a shorter duration rather than reduce the actual duration of trips. At first, visits to water become less frequent, reaching a minimum in July (Figure 17b). During this period, elephants prefer making 48h or 72h trips rather than 24h or 5h (Figure 17c). While daily maximum temperature remains below 25°C (Figure 17a) elephant's drinking requirements remain low as well. However, smaller natural water pans disappear early in dry season meaning elephants already need to make long trips to and from larger water pans to maximize their foraging opportunities. From August to October the number of visits increases twofold as maximum temperatures rise up to 35°C or more (Figure 17a). 72h trips virtually disappear and the number of short trips increases fivefold (Figure 17c). Surprisingly, trip duration is remarkably constant within each period and throughout the dry season (as described in appendix 2). However, there are two exceptions: short looping trips become briefer as the dry season progresses and 48h looping trips are a couple of hours shorter during the hot dry season. Nonetheless, these exceptions are not sufficient to explain the fivefold increase of the number of short commuting trips during the hot dry season. Although short trips appear critical to adjust drinking frequency, their short duration implies elephants remain close to water during these trips. Hence, changes in these trips have little impact on how elephants deal with usage of areas further away from water.

We will focus on 24h and 48h trips to explore how elephants cope with growing spatial constraints throughout the dry season. In total, these trips account for more than 80% of elephant's time budget, the role of short trips to adjust for drinking will be described separately, unfortunately there were too few 72h trips to assess whether there were any significant trends.

3.2 24h trips

Elephants travel 2.3 - 4.6 km away from water during 24h trips. Maximum distance to water increases on average by 1km during the dry season (Figure 18 c,d) but trip duration remains unchanged (Appendix 2). This is achieved by doubling returning speed during the transition from the cold to the hot dry season (Figure 20c) followed by the doubling of outgoing speed during the peak of the hot dry season (Figure 20a). However, elephants may increase traveling speed for different reasons whether they are making commuting or looping trips. At the onset of the dry season elephants probably spend a substantial part of 24h commuting trips foraging since the distance travelled is more than twice the beeline distance between waterholes. However, the increase in trip straightness in July and August implies that during the entire hot dry season commuting trips are at most 40% longer than the direct distance between waterholes. This suggests that changes in 24h commuting trip speed and distance to water reflect the necessity to reach waterholes that are further away from each other rather than

actual foraging decisions. Conversely, during looping trips, elephants appear to travel directly to a given foraging site and back as shown by the high yet unchanging straightness index (Figure 21d). Nonetheless, increasing travelling speed (Figure 20 a,c) enables them to travel on average 1km further by the end of the dry season (Figure 18 d).

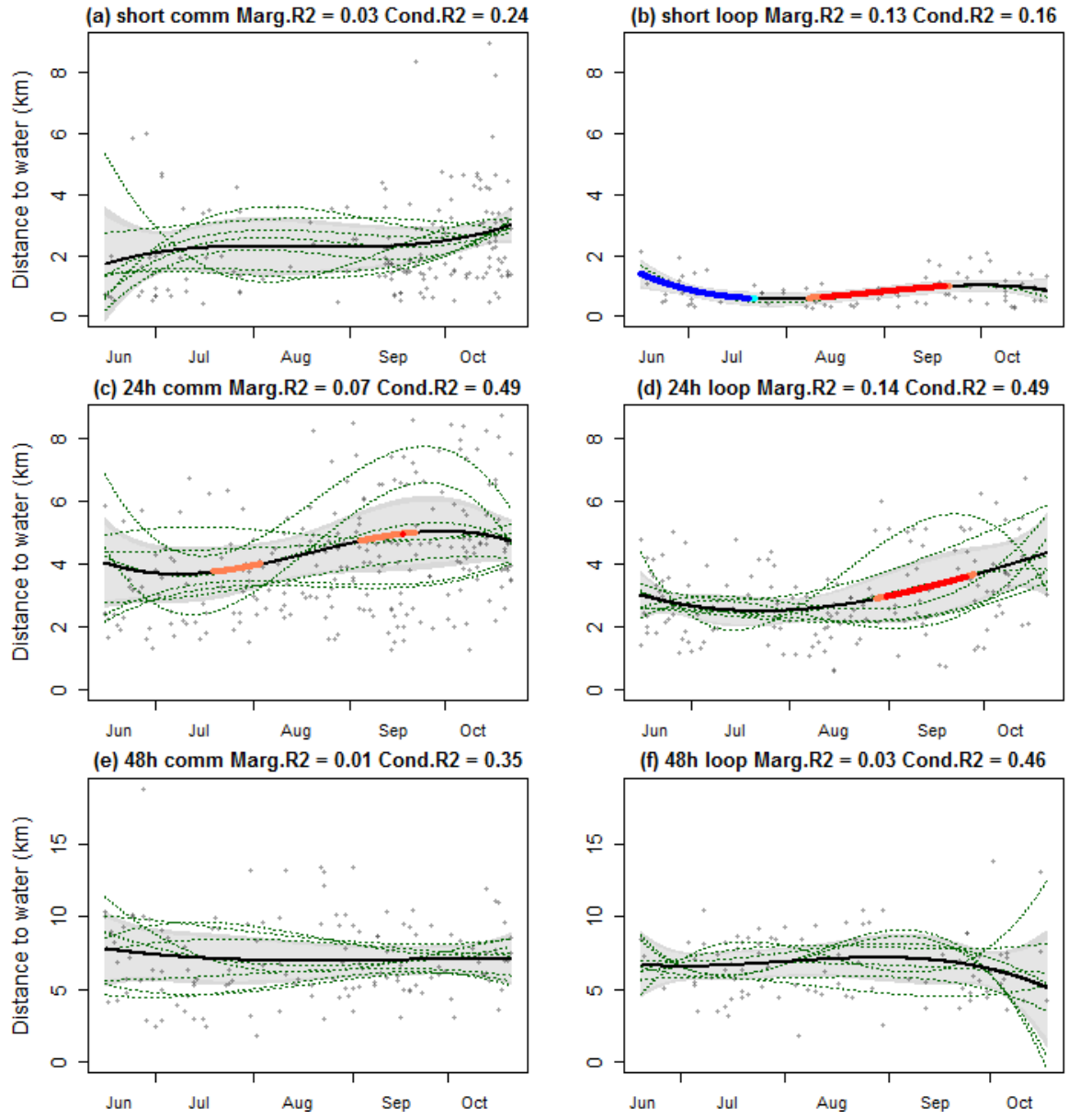


Figure 18: Maximum distance to water during short trips (a,b), 24h trips (c,d) and 48h trips (e,f). Left panels show commuting trips (a,c,e) and right panels looping trips (b,d,f). Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects.

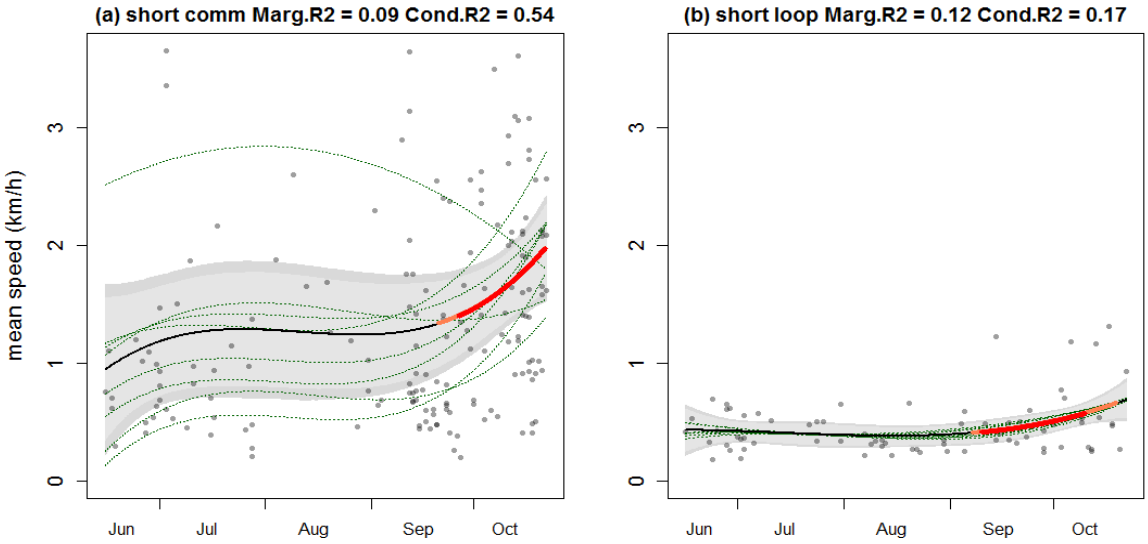


Figure 19 : Average speed of short trips. (a) commuting and (b) looping trips. Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects

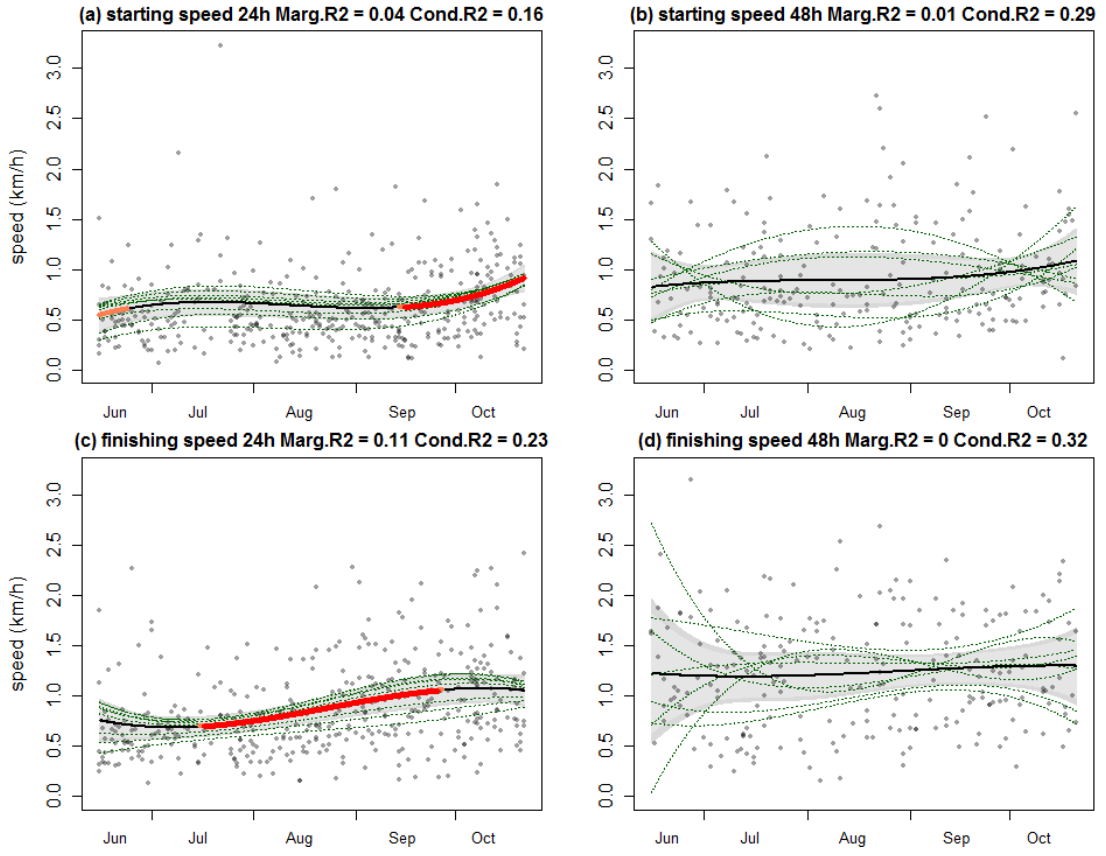


Figure 20. Average outgoing and returning speed of 24h trips (a,c) & 48h trips (b,d). Outgoing speed (and returning) speeds were averaged over the first (respectively the last) 3h of the trip. Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects

3.3 48h trips

Elephants travel twice as far during 48h trips than 24h trips. They reach 5.0 - 8.7 km on 48h trips (Figure 18) and 10.1 - 13.8 km on 72h trips (data not shown). Unlike 24h trips, distance to water does not change during the dry season for 48h trips for either commuting (Figure 18 e) or looping (Figure 18 f). Outgoing and returning speed do not change either. However, these speeds are consistently higher than for 24h trips at 0.9 km/h for outgoing speed and 1.2km/h for returning speed suggesting elephants reach their maximum speed and distance during these 48h trips (Figure 20 b,d). Whereas 48h looping trip straightness are similar to 24h looping trips, commuting trip straightness was much more variable between trips and throughout the season (Figure 21 e,d). The increase in straightness in July and August may be attributed to increasing distance between waterholes. During the peak dry season straightness decreases for most individuals suggesting elephants are less constrained by waterhole location in their foraging decisions during 48h trips.

3.4 Short trips

The seasonal trends for short commuting trips are largely driven by their fivefold increase during the hot dry season. High baseline average speed (>1 km/h) and the increase to nearly 2km/h) during the hot dry season suggests little or no foraging occurs during these trips. Furthermore, these trips had the highest straightness throughout the dry season from the initial increase from 0.7 to 0.8 in June up to nearly 0.9 in October. Unlike short commuting trips the seasonal trends in short looping trips are consistent with longer 24h or 48h. The initial decline in distance to water may be due to a shortening of trip duration and the subsequent increase can be attributed to higher travelling speed since trip straightness remained constant. Thus the increase in average speed during the peak of the dry season may indicate a reduction of the time spent foraging during these trips. Yet the consequences on foraging of these adjustments are limited since these trips tally for less than 2% of elephants' time budget.

4 Discussion

4.1 The advantages of travelling faster and straighter

As the dry season progresses elephants appear to mitigate the trade-off between foraging far away in probably more profitable locations and drinking often by increasing travel speed and trip straightness (Figure 22). By doing so, elephants travel further away from waterholes but maintain foraging time and increase drinking frequency when conditions become more adverse. These results question the basic assumption made by most central place foraging models that, all else being equal, the average rate of energy gain declines when animals forage further (Olsson, Brown & Helf 2008). Indeed, by omitting travel speed such models assume there is a strict linear relationship between the distance to a patch and the time it takes to reach it. However, the energetic costs of travelling do not scale linearly with travelling speed and are particularly low for large bodied species like elephant (Langman et al. 1995). Further

models allowing travel speed to vary may reveal it is advantageous for elephant to increase travelling speed and the associated metabolic costs in order to improve their foraging opportunities.

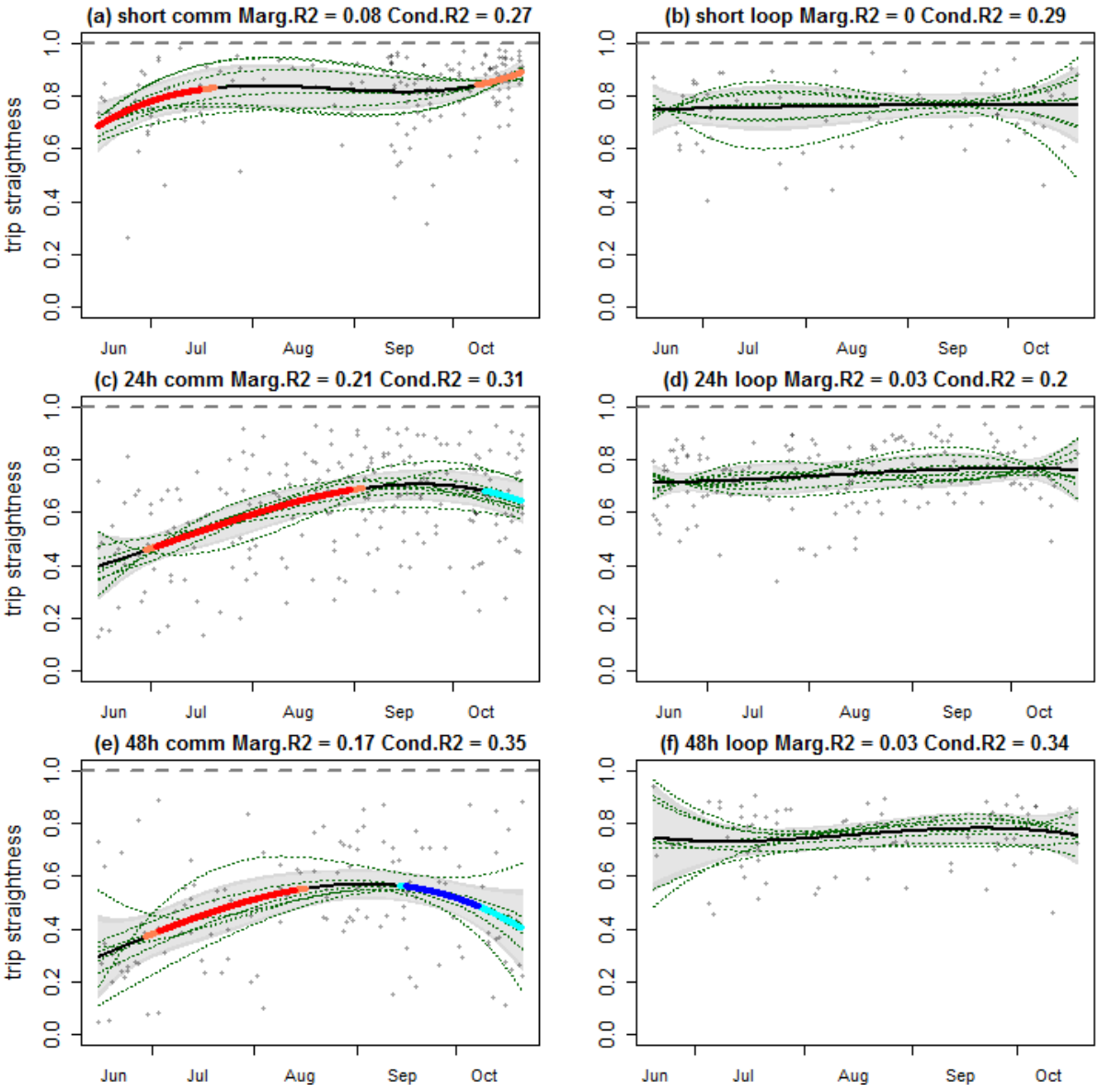


Figure 21: Trip straightness during short trips (a,b), 24h trips (c,d) and 48h trips (e,f). Straightness = beeline distance / total distance for commuting trips (a,c,e left pannels) and Straightness = 2xmaximum distance to water / total distance for looping trips (b,d,f, right pannels). Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects.

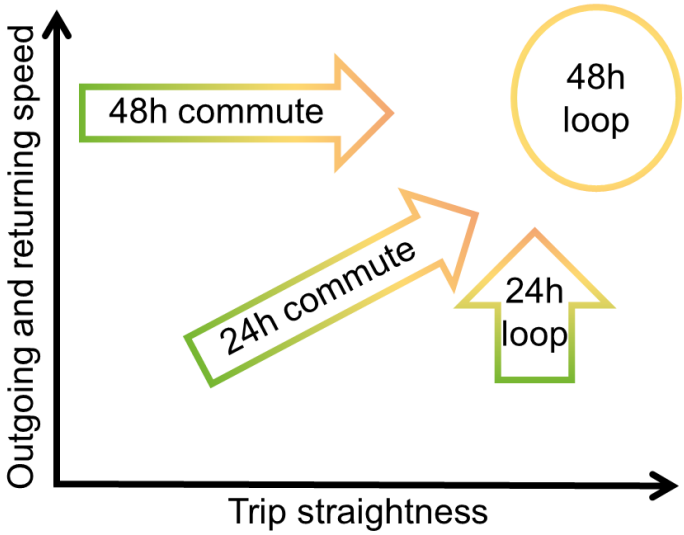


Figure 22: Schematic representation of the convergence of trip straightness and speed throughout the dry season (green-> brown). Returning speed increased earlier than outgoing speed.

Elephant's hurried directed movements to and from foraging patches in Hwange NP throughout the dry season reflect the structure of their environment. Herbivores consumption of vegetation surrounding water sources creates a piosphere (Lange 1969; for a review see Thrash & Derry 2008). From the herbivore's perspective foraging resources decrease dramatically close to water due to structural changes in the vegetation, that have been described in Hwange NP (Chamaillé-Jammes, Fritz & Madzikanda 2009), and forage depletion. From the onset of the dry season elephants appear to maximize time spent far away from water by making directed outward movement followed by a directed return that result in high looping trip straightness (Figure 21). By travelling further to patches with higher available biomass, elephants could increase their intake rate sufficiently to reduce the time needed to meet their energetic requirements and make up for the extra travel time (Bergman et al. 2001). Higher travelling costs during the dry season may be compensated by a shift in their dietary preference to increase energy intake (Pretorius et al. 2012). By choosing these remote but more rewarding patches over closer poor quality patches they reduce missed opportunity costs (Brown 1988; Shrader et al. 2012). Thus elephants may actually save time and increase their total intake by travelling further during 24h trips. The absence of change in 48h trips may indicate that piosphere effects dwindle beyond 7 km from water or that elephants have already reached their maximum speed and straightness during these trips at the onset of the dry season (Figure 22). Alternatively, the absence of change in 48h trip parameters may result from landscape constraints. There were no areas beyond 15 kilometers from water in elephant's dry season home-range (Figure 16). Thus, elephants had no need to go any further on 48h or 72h trips following their large scale landscape preference. However such patterns may emerge in other systems with larger distances between waterholes.

Although adults are unlikely to suffer from predation, family groups are wary of lions (*Panthera leo*) that can effectively capture and kill elephant calves especially during the hot dry season (Loveridge et al. 2006; Davidson et al. 2013). Predation risk is highest within the first two kilometers of water (Valeix et al. 2010) suggesting it would be advantageous for elephants to minimize time spent in the vicinity of water. However, it is unlikely predation risk is one of the main drivers of central place effects of waterholes on elephants since they prefer coming to drink at dusk (Appendix II) when predation risk is highest throughout the dry season (Valeix, Chamaillé-Jammes & Fritz 2007).

Foraging theory, and particularly missed opportunity costs, provides a framework to understand elephants' movement patterns throughout the dry season. However, energetic constraints apply on the long term: elephants, like most large herbivores, gradually deplete their body reserves during the dry season. Is the energetic balance sufficient to understand why elephants actually move faster and travel further as the dry season advances or do short term costs, with immediate risks hyperthermia prevail?

4.2 The currency of foraging decisions: thermoregulation or energy gain?

The number of visits elephants made to waterholes was surprisingly well correlated with seasonal temperature variations (Figure 17). Elephants visited waterholes less often when temperatures were low during the cold dry season and returned to drink more frequently as temperatures rose during the hot dry season. Over recent years, temperature has emerged as one of the key determinants of elephant foraging decisions. In Kafue NP, Zambia, elephants select cooler habitats when temperatures rise (Kinahan, Pimm & van Aarde 2007). Similarly, in Hwange NP elephants avoid being active during the heat of the day during the hot dry season and prefer travelling to water later in the evening (Valls Fox & Chamaillé-Jammes unpublished data). Despite these behavioral adaptations, even for temperatures as low as 10°C-12°C, evaporative cooling is the main thermoregulatory process used by elephants (Dunkin et al. 2013) confirming the tight link between ambient temperature and drinking. Adult African elephants can drink over 200 L a day (Olson 2002). We found elephants visit waterholes on average once a day at the peak of the dry season in October which is consistent with the water debt of 100 $L.day^{-1}$ predicted by Dunkin et al under similar climatic conditions. Elephants do spend roughly half of their time making 24h trips. However, they continue making longer trips lasting 48h or even 72h throughout the hot dry season potentially accumulating a water debt that may surpass the amount of water they can absorb during a single visit to a water pan. Indeed, these longer trips are generally followed by a succession of 1 or 2 short trips (data not shown). These patterns suggest elephants alternate periods of water deficit to access remote foraging areas with successive drinking bouts to readjust their osmotic balance. If so, the variance of elephant core body temperature should increase with trip duration indicating a water deficit (Hetem et al. 2014). Alternatively, successive visits may correspond to failed drinking attempts due to exacerbated intraspecific competition (Valeix,

Chamaillé-Jammes & Fritz 2007) or predation risk at the end of the dry season (Davidson et al. 2013).

4.3 Landscape complementation a driver of elephant movement

Elephant movement patterns vary seasonally. Several studies have shown that elephants move more, have larger home-ranges and exhibit lower site fidelity during the rainy season than during the dry season (Paper *et al.* 2007; Loarie, van Aarde & Pimm 2009). Greater elephant mobility is generally explained by the absence of water limitation and broad-scale preference of habitats with the highest seasonal productivity (Young, Ferreira & Van Aarde 2009; Marshal *et al.* 2010; Wall *et al.* 2013; Bohrer *et al.* 2014). When unconstrained by surface water availability, elephants appear to become nomadic within their wet season range as they track vegetation growth following rainfall events (Garstang et al. 2014). During the dry season, elephant movement is constrained by surface water availability which leads movement models to predict a strong preference for areas within a few kilometers from water (Paper *et al.* 2007; Harris *et al.* 2008). Recently, detailed analyses of fine scale movement confirmed the importance of directed movement to and from water (Polansky, Kilian & Wittemyer 2015) and revealed preference for habitats close or far away from water depended on the elephant's behavioral state (Roever et al. 2014). In African savannas surface water and forage become non-substitutable resources during the dry season. In a natural experiment in Namibia, Legget (2006) reported that elephant family herds previously seen on 96% of occasions within 10km of permanent water source were no longer found on more than 2% of occasions after the installation of artificial water points enabled them to shift their dry season home-range. In our study, we applied the concept of landscape complementation (sensu Dunning et al. 1992) to tease apart the roles of surface water availability and forage availability as drivers of elephant movement.

At a large scale landscape effects can be seen at the population level: elephant densities increase in areas with higher waterhole density (Chamaillé-Jammes, Valeix & Fritz 2007; De Beer & Van Aarde 2008). Higher elephant densities in these areas result from the contraction of elephant breeding herds home-ranges during the dry season (Figure 16). The Hwange elephant population nearly doubled after culling came to an end in 1986 and has remained around 40 000 individuals since the late 1990's (Chamaillé-Jammes et al. 2008, Chamaillé-Jammes et al. unpublished data). Despite this increase and the substantial vegetation changes due to elephants (Valeix *et al.* 2007), elephant movement patterns are remarkably similar to a previous telemetry study, before the culling ended, spanning from 1980 to 1983 (Conybeare 1991). As reported by Conybeare, elephants preferentially range 3-10 km from water during the dry season and always remain within 15km of water. Elephants may range much farther; family groups in the Namib desert have been reported to regularly travel 20-40km from water (Viljoen 1989). During our study one migratory group walked 125 km across the park over a 5 day period after water disappeared from its wet season home-range. Yet, elephants choose to remain in landscapes that provide both food and water within 15km from one another.

Missed opportunity costs may be too high in Hwange for elephants to go further because they may not find more rewarding patches beyond 15km from water due to intraspecific and interspecific competition. In addition, elephants may prefer remaining within a day's travel distance of several waterholes rather than relying on a single artificial water source that may suddenly dry up, be overcrowded or occupied by predators.

Within their dry season home-range the pattern appears to be reversed. Elephants actively avoid areas close to water by making directed and rapid movements away from waterholes during their foraging trips (Figure 19Figure 20). Studies showing that elephants moved less during the dry season than during the wet season made the arbitrary assumption that elephant movement patterns were homogenous during these time periods. We found substantial changes in elephant movement patterns throughout the dry season and hypothesized these resulted from (i) increasing temperatures, (ii) forage depletion around waterholes, and to a lesser extent (iii) longer distances between waterholes. In a recent study Birkett et al. (2012) established elephant travelling speed increases during the dry to wet transition period and then decreases during the wet to dry transition. The authors attempt to correlate the change in ranging behavior with the first rainfall event and subsequent vegetation flush that would attract elephants over large distances. We chose to end our study on the day of the first major rainfall and did observe a gradual increase in speed and travelling distance for several months before the end of the dry season (Figure 18Figure 19Figure 20). Therefore, we believe greater mobility at the end of the dry season and during the early rains may result from two processes. Initially, elephants travel faster and further from water to escape from the piosphere effect. Once the rains start in earnest, this effect is superimposed to the transition period during which elephants can move to their wet season home-range because they are no longer constrained by water availability but they must nonetheless range afar in search of patches of early regrowth.

The contraction of water dependent herbivores around this key resource appears to be ubiquitous in semi-arid and arid systems. However the small scale patterns we observe result from the spatial segregation of drinking and foraging resource patches. The ranging patterns we describe for elephants are therefore more likely for populations that occur at large densities or that are weak competitors making them sensitive to resource depletion. Piosphere effects caused by elephants have been reported extensively throughout African savannas (Ben-Shahar 1993; De Beer *et al.* 2006; Valeix *et al.* 2007; Gaugris & Rooyen 2010; Fullman & Child 2013; Fullman & Bunting 2014). As such, distance between waterholes may be the key determinant of small scale movement patterns in dystrophic systems relying on artificial waterholes like Hwange National Park. Thus, the patterns may only hold in ecosystems where a significant part of the home-range is more than 5 km or perhaps 10km from water. In other systems it may not be necessary for elephants to alternate long 24h, 48h, or even 72h foraging trips with short "drinking" trips. For example, elephants in Kruger NP may have very different patterns: They prefer coming to drink at midday rather than at dusk

(Hayward & Hayward 2012). They spend on average o 18h away from water and remain a substantial part of their time foraging in riparian thickets forests alongside perennial rivers (Thaker and Vanak pers. comm.). In addition, waterhole use by herbivores also depend on human activities for example, all herbivores prefer to come to drink at night in areas where they are subjected to hunting around Hwange NP (Crosmary et al. 2012b). Finally, ambient temperatures have a substantial effect on elephant activity patterns (Kinahan, Pimm & van Aarde 2007). Similar movement responses to drinking and foraging trade-offs are therefore more likely in hotter and dryer environments, systems with artificial water provisioning that lack riparian habitats that may change movement patterns by serving as key foraging areas during the dry season and risky drinking opportunities due to predators or human activities.

5 Conclusion

The distribution of foraging resources and surface in water shape elephant movement patterns throughout the dry season. They establish their dry season home-range in areas that provide both resources within commuting distance. Elephants appear to optimize their provisioning strategy early on by heading out fast and straight during their foraging forays. As temperatures increase, elephants return to drink more often. However elephants continue to exploit remote patches by alternating long 48h foraging trips with short (5h) commuting trips. Simultaneously, intermediate 24h trips become more similar to longer 48h trips as returning speed and finally outgoing speed increase. They also use their navigation capacities by travelling straighter during commuting trips. As a result, short term thermoregulatory and feeding constraints determine elephant's response. Elephants increase travelling and thus energy expenditure during the time of the year when mortality for both adult and young is highest.

Elephants restricted their range to areas located within 15km of water. The areas within 15km of water define the elephant population's dry season home-range. Managers could use the 15km limit to determine the ratio between the dry season area and the rainy season area to regulate the elephant population. Targeted water provisioning within areas usually beyond 15km from water during droughts might reduce inter-annual resource fluctuation for large herbivores.

6 Appendix I Method to detect visits to waterholes.

6.1 Visit detection

Two metrics were used to detect an individual's visit to a given water pan: a buffer (i) and a "coming" index (ii) (Figure 23). (i) An individual was considered to have visited a waterhole if its GPS track intersected a buffer of a given radius. In practice this was done by linearly interpolating the movement track. In order to avoid detecting spurious visits, if two consecutive visits were detected within a tolerance interval they were merged into one visit unless it was a different waterhole. The threshold was set at 40min which ensured the individuals never really had time to leave the proximity of a given waterhole during such a time period. (ii) We also considered a visit had occurred if an individual was "coming" to water. Let us consider an individual is moving towards a waterhole. At a given relocation we assume it maintains the same speed and direction as during the previous time step. A visit was detected if a waterhole could have been reached under this assumption. In other words: the distance to the waterhole was smaller than the distance to the previous location along a distance to water axis. Geometrically, if one considers two consecutive relocations at times t and t+dt, and $D_w(t)$ the distance to water of a given relocation, there was a visit if:

$$D_w(t+dt) < (D_w(t) - D_w(t+dt)) = \Delta D_w.$$

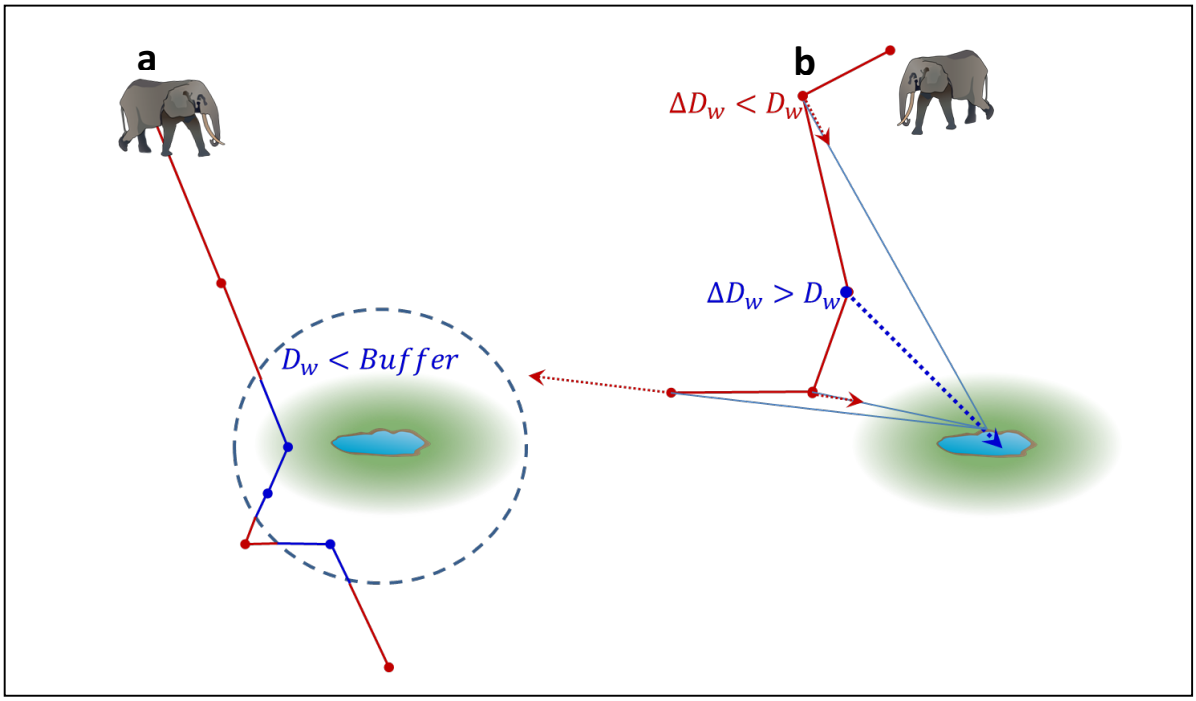


Figure 23: Illustration of the two methods used to identify visits. (a) A visit is considered to have occurred if an individual enters buffer centered on the waterhole. (b) Alternatively, a visit can be detected if the net displacement in direction of the waterhole between two consecutive locations is greater than the distance to the waterhole of the second location.

6.2 GPS calibration

In order to assess the validity of both indices collars were set to record one point every 5 minutes during a four day period in October 2013. We retained data from ten collars for which success rates during these four days exceeded 90 % and did not have any gap longer than 30 minutes (Figure 24).

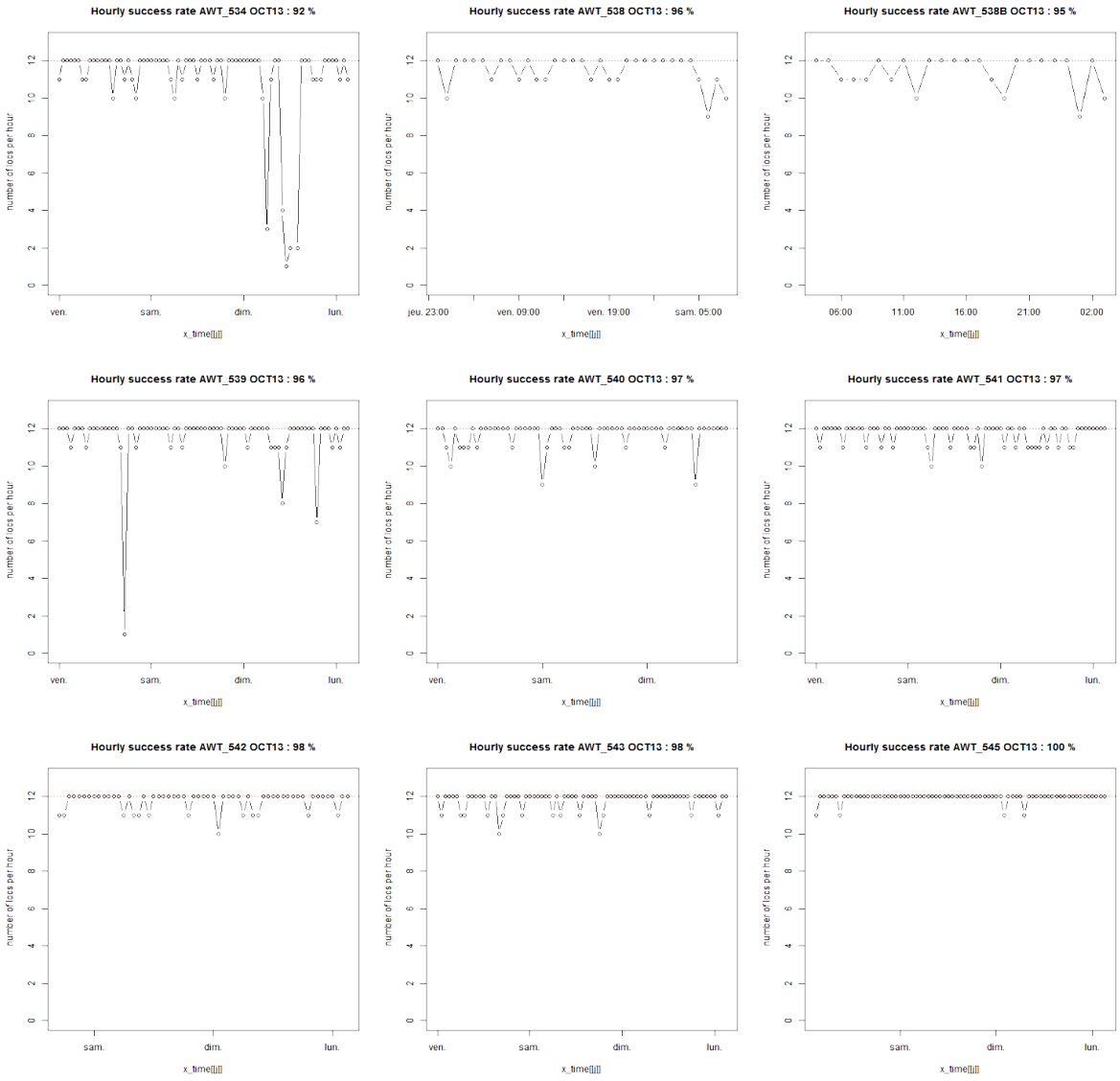


Figure 24: Hourly success rates while the collars were programmed to obtain a GPS location every 5 minutes. The sequences for collars 538 and 548 were split in two sections that were used independently due to a large gap during the experiment.

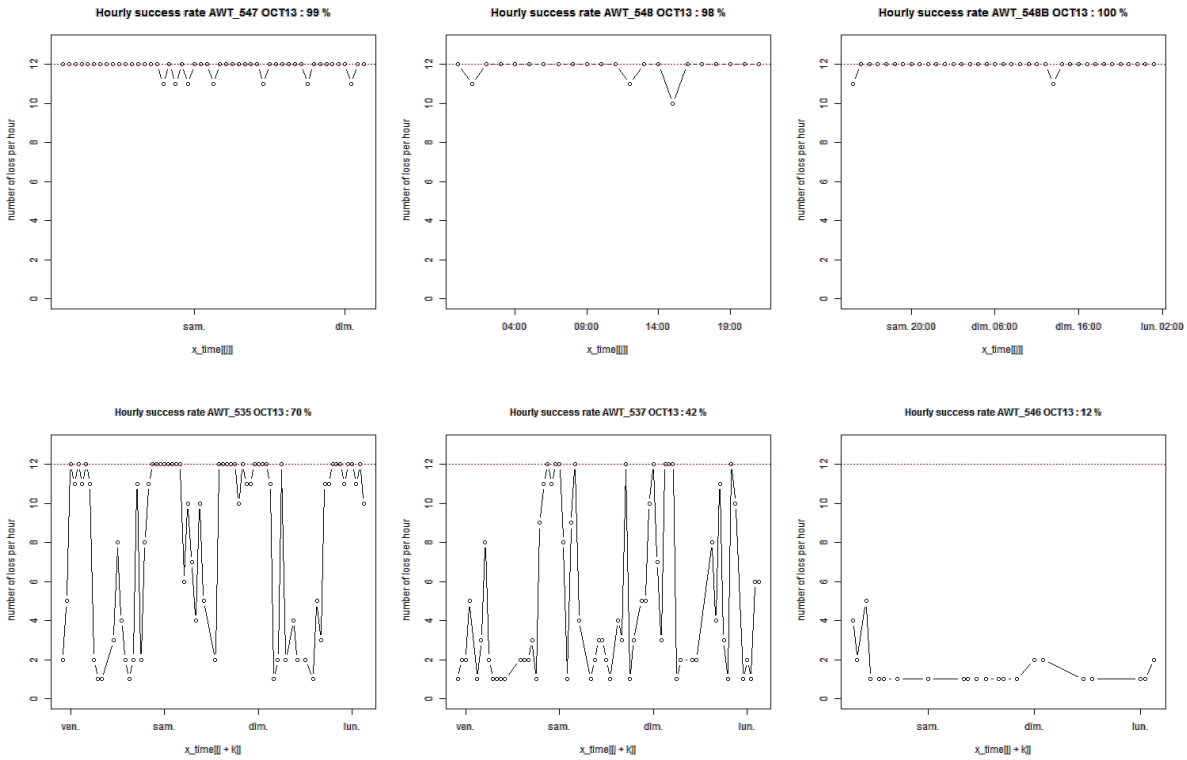


Figure 24: (continued) Hourly success rates while the collars were programmed to obtain a GPS location every 5 minutes. The success rates were <90% for collars 535, 537 and 546 shown in the lower panels they were therefore discarded.

Most pans are roughly circular in shape with a diameter ranging from c. 20m – 100m at the time of the study. Distance to a water pan was therefore considered to be equivalent to the distance to its centroid. The Buffer was set at 200m since it would have been unrealistic for an individual to enter the buffer, drink and exit the buffer in 5 minutes. Elephants walk fastest just before reaching water pans (Chamaillé-Jammes et al. 2013), in October 2013, the longest distance covered over a 5 min period was 450 m (5.4 km.h-1). The consistency of visits was subsequently proof checked by a visual inspection of the trajectories in Quantum GIS 2.4.0. To assess the accuracy and sensitivity of our parameters, the reference visit sequence was compared with visits identified using increasingly large buffers (100m – 1400m) and long GPS fix rate intervals (15 min – 3hrs) obtained by subsampling the high frequency reference trajectory (Figure 25Figure 26).

39 visits were identified for 10 individuals when the success rate was above 90%. These visits were thereafter considered as the real visits and taken as a reference. With the default fix rate of 30 minutes and a conservative 200m buffer, the combination of both methods enabled us to detect all 39 visits. 95% of visits were found by the coming index and 85% by the buffer (Figure 25Figure 26). There was only one false positive (2.5%) however upon visual inspection of the sequence the track veered away from the water-point less than 500m before reaching it while moving at high speed (3km.h-1). As expected when the fix rate decreased to 60 min

or 90 min visit detection decreased to 90% and 87% respectively (Figure 25) this would correspond to missing one or two consecutive locations.

At any given sampling frequency increasing buffer size increased the proportion of visits detected by the buffer until all visits were detected. This occurred at 850 m for a 30min fix-rate and 1.2 km for the 60 min fix-rate. Increasing buffer size significantly increased the chances of detecting a visit for small buffers. However, the slope typically saturated beyond 300m-400m. Increasing buffer size also generated two undesirable errors: false visits and merged visits. Whereas a small proportion of false visits seemed inevitable as sampling frequency decreases (Figure 26) their number steadily increases with buffer size beyond a 400m threshold. Merging visits can lead to a loss of information since two consecutive visits to a waterhole are subsequently treated as one. This can partially compensate the occurrence of false visits since individuals are generally found close to water pans just before or just after a real visit.

Whereas both methods were sensitive to sampling frequency (Figure 26) the coming method was hardly affected by buffer size (Figure 25). The coming method detected up to 30% more visits than the buffer for a 200m buffer, it was below 20% for a 400m buffer and below 10% for a 600m buffer (Figure 25). However there always was a constant 5%-10% portion of visits that were not detected by the coming index. Both criteria are complementary: The buffer identifies visits with greatest accuracy when the individual moves slowly but the coming index does not. When the individual moves fast, no locations fall within the buffer but the coming index identifies visits readily. The coming index could also compensate small gaps in the data with one or two missing relocations.

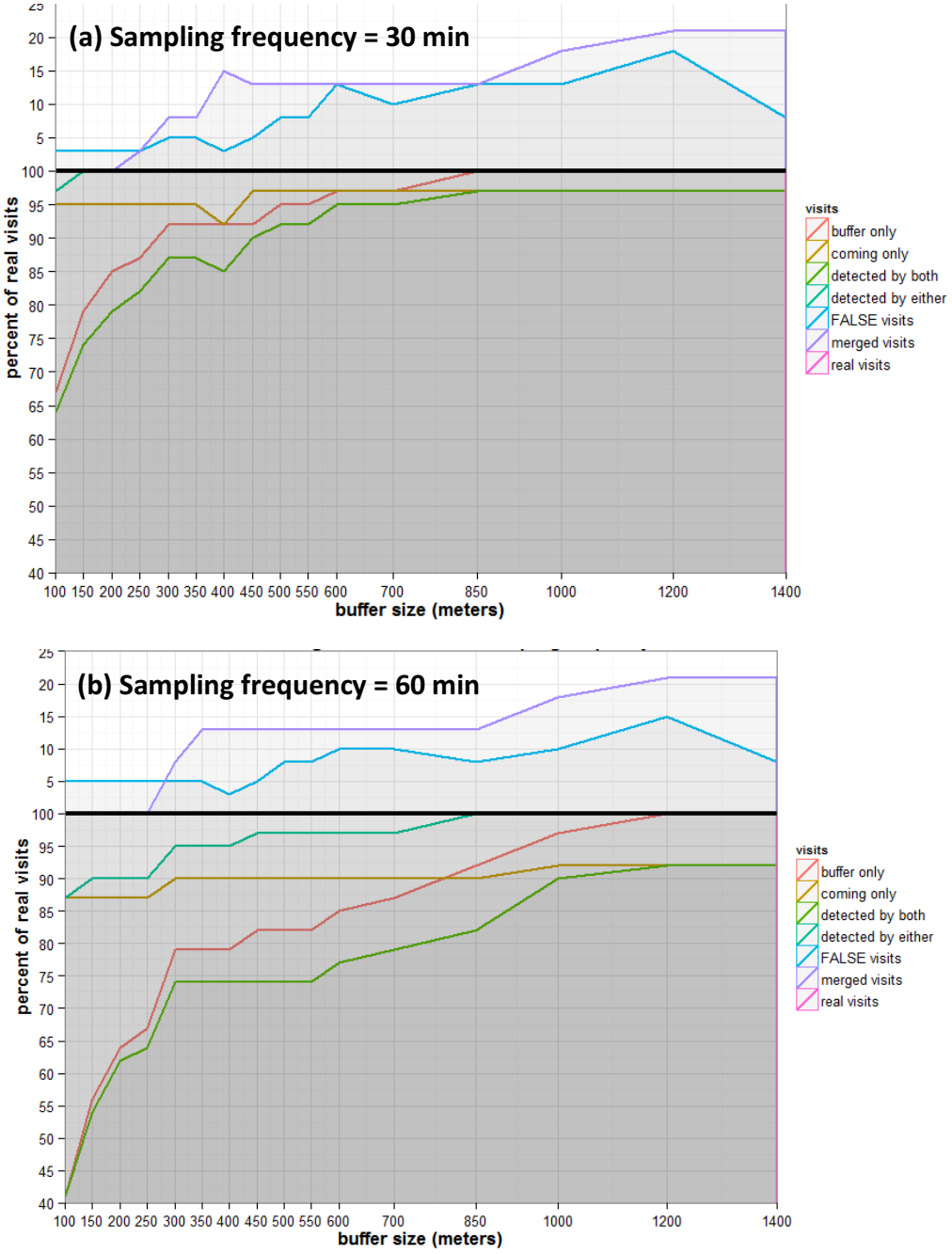


Figure 25: Percentage of visits detected according to buffer size for a 30 min fix rate (a) and a 1 hour fix rate (b). The lines below the black reference line (100%) represent the percentage of visits detected by both indices (green), by the buffer (orange), by the coming index (brown), by either the coming index or the buffer (blue green). Note that all visits were detected by at least one method when the buffer was larger than 150m with a 30min fixrate and 850m with the 60min fixrate. The lines above the reference lines indicate two other kinds of errors: False visits (purple) and merged visits that occurred when the individual did not exit the larger buffer for more than 40minutes between two consecutive visits.

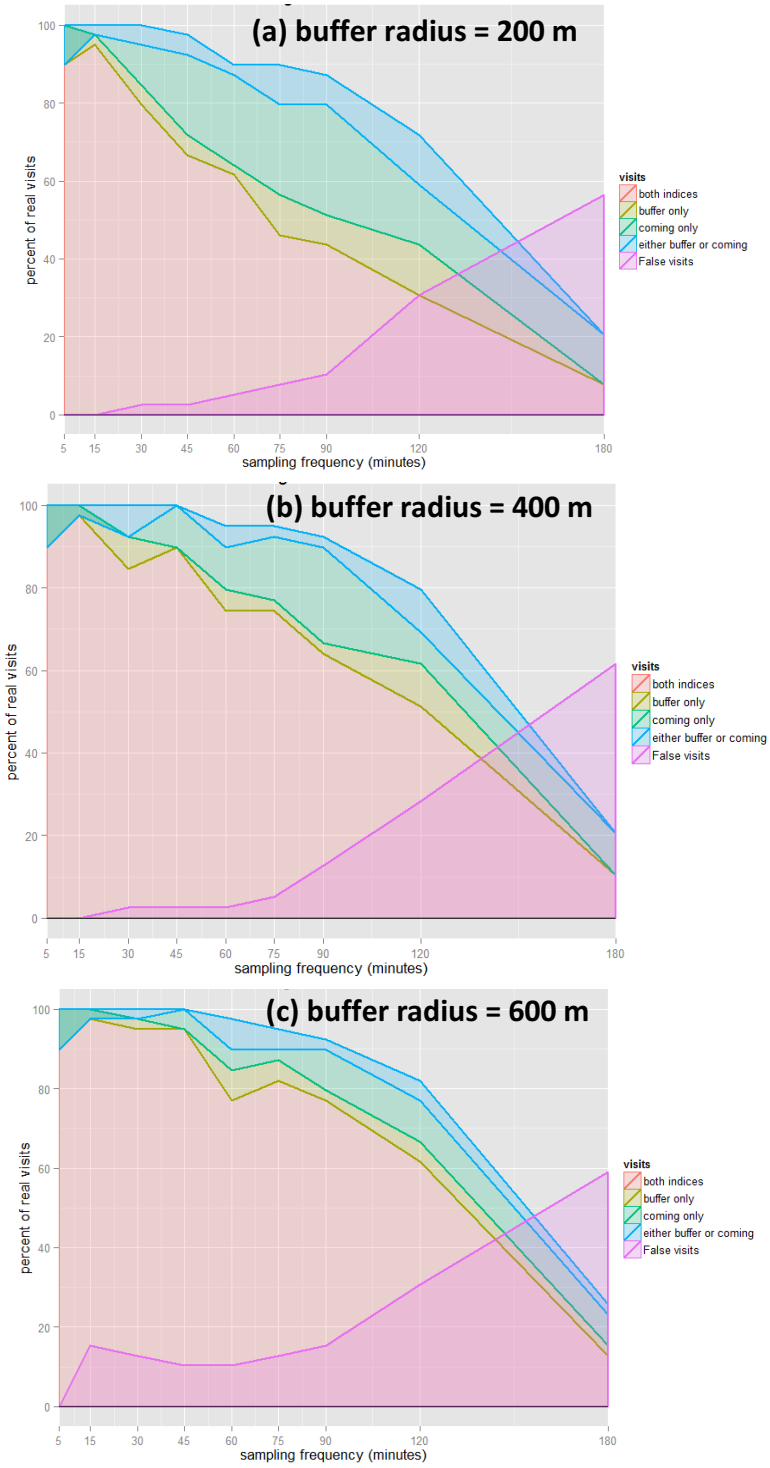


Figure 26: Percentage of visits accurately detected according to sampling rate for 200m (a), 400m (b) and 600m (c) buffers. For each buffer size, the we calculated the percentage of visits detected by either method (blue), by the coming index (green), the buffer only (brown) and both methods simultaneously (pink). The purple line show the increasing number of false visits as buffer size increases and sampling rate decreases.

6.3 Field validation

Visits to waterholes were independently validated using direct observations in the field and camera traps. When a group of elephants was spotted at a waterhole, a positive identification of the collared individual was inferred using the VHF signal and confirmed through direct visual observation of the animal with a collar. Reconyx Hyperfire Camera traps were deployed at 19 waterholes for 50 sessions of 5-13 days amounting to 433 days of observation. The cameras were set at a distance from the water's edge in order to encompass the entire pan within the image; one picture was taken every 20seconds from dawn to dusk (Figure 27). Visits were confirmed when a single group of elephants came to the pan between the two closest GPS locations to the waterhole or if there was a positive identification of the collared individual on a photograph. In the case of cattle, visits were confirmed by the herd boys during short interviews conducted after each tracking session.

In total 12 visits were confirmed through direct observation (Table 1) and 28 with camera traps (Table 2). Out of 127 visits that occurred during the camera trap sessions, only 28 visits could be validated because elephants prefer drinking at night (80 visits) or are so numerous that the group with the collar cannot be singled out (19 visits). In one instance a visit was erroneously detected at Ngwenya 2, however the elephant herd appeared to have entered the 200m buffer on its way to Ngwenya 1 waterhole situated at 800m from Ngwenya 2. No negative controls were made since these would imply following elephants for lengthy periods off roads in dense bushland and woodland thickets.

Table 1 Opportunistic sightings: 12 opportunistic sightings of 6 different collared individuals at 10 different water pans throughout the dry season were used as independent field validations.

id	date	waterhole	detected	seen
534	20/07/2013	Sinanga	17:30 - 18:30	~ 17:30
534	14/10/2013	Nyamandhlovu	10:14 - 10:19	~ 10:00
534	14/10/2013	Dom	13:14 - 13:19	13:20 - 13:26
534	29/10/2013	Tshebe Tshebe	16:09 - 16:49	~ 16:05
537	28/05/2013	Balla Balla	15:39 - 16:19	~ 16:12
538	04/10/2013	Dopi	16:36 - 17:46	16:41 - 17:29
540	11/10/2013	Caterpillar2	16:45 - 17:00	~ 16:49
542	05/07/2013	White Hills	12:06 - 12:46	~ 12:35
542	09/09/2013	Dom	17:40 - 18:15	17:40 - 17:49
542	12/09/2013	Livingi	13:30 - 17:05	16:38 - 16:53
542	20/09/2013	Livingi	12:10 - 13:10	12:55 - 13:05
545	17/06/2013	Nyoka	14:41 - 16:26	15:19 - 15:22

Table 2 Camera traps by individual and water pan. The quality of the observation were rated as: "collar", "drank", "maybe" or "no". "Collar" indicated collar was visible on the photographs (eg; Figure 27). If there was no ambiguity concerning the identification of the group and the time of the visit but the collar could not be seen on the photograph we rated the observation as "drank". "Maybe" were discarded because the group with the collar may have been one of several visiting the waterhole within the same time window. "No" occurred when no elephant came to drink at the waterhole.

	id	N obs.	waterpan	N valid	validation	N valid
	534	2	Balla Balla	2	collar	7
	535	9	Caterpillar 2	1	drank	20
	537	2	Dom	14	maybe	19
	539	1	Hobo	1	no	1
	540	7	Livingi	6		
	542	9	Ngwenya 2	5		
	543	7	Nyamandhlovu	16		
	545	2	Tshebe Tshebe	2		
	547	2				
	548	6				
total	**10**	**47**	**8**	**47**		**47**

Figure 27: The needle in the haystack, Camera trap photograph of a collared elephant cow leaving Livingi waterhole, Hwange NP at 14:09:20 (top panel) and 14:09:40 (bottom panel). In this image there are about 50 individuals but there may be more than 200-300 elephants simultaneously drinking at pumped waterholes.

7 Appendix II Factors explaining the variability of trip duration throughout the dry season

One of the key features of elephant movement patterns in Hwange National Park is the periodicity of visits to waterholes. It has long been known that Hwange elephants prefer coming to drink at dusk (Valeix, Chamaillé-Jammes & Fritz 2007). However the complexity of movement patterns around water have only recently come to light (Chamaillé-Jammes et al. 2013). Foraging trips can be classified as looping trips when elephants return to the same waterhole or commuting trips when they change waterhole. In addition trip duration is multimodal: Elephants will either make short (5h) trips, 24h, 48h or 72h trips (Figure 28).

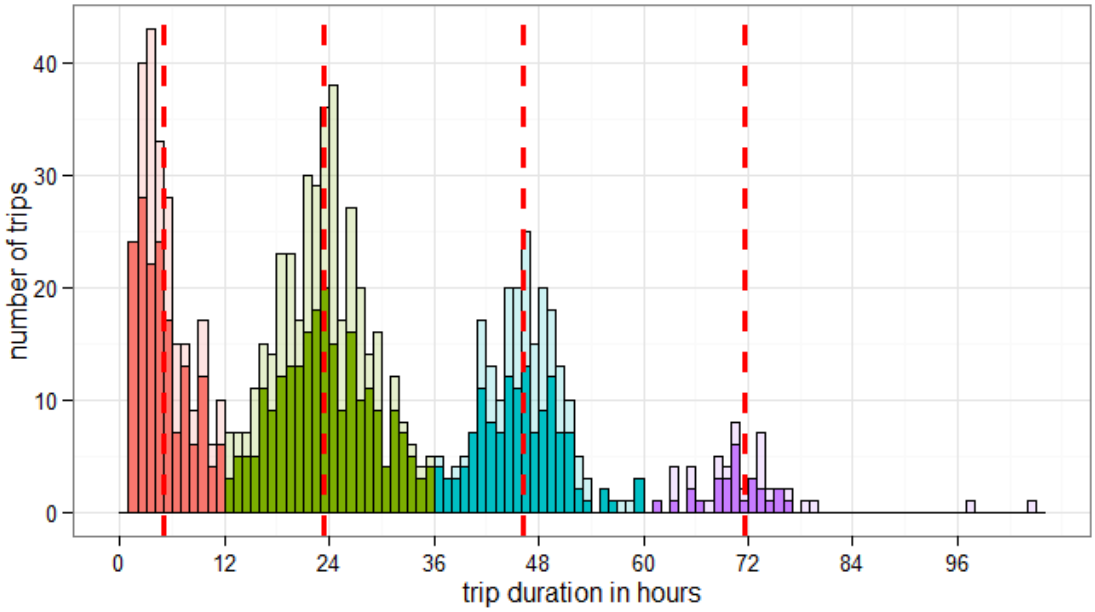


Figure 28: Foraging trip duration is multimodal for both looping trips (light bars) and commuting trips (dark bars). Elephants make short trips (mean=5h, sd=3h), 24h trips (mean=23h, sd=5h), 48h trips (mean=46h, sd=4h), 72h trips (mean=72h, sd=7h). Out of 901 trips we recorded only 2 four day trips that lasted 98h and 105h respectively. Mean trip duration is shown by dashed vertical red lines for each mode.

7.1 Trip duration throughout the dry season

Surprisingly trip duration remains unchanged for commuting trips throughout the dry season (Figure 29 a,c,e). Trip duration remained unchanged for 24h looping trips (Figure 29d) but decreased during the hot dry season for 48h trips (Figure 29f). Short looping trip duration become shorter, there is a significant decrease at the beginning and the end of the dry season. The small increase in august is most likely to result from the adjustment of the third order polynomial to the early and late dry season decreases rather than an actual change in elephant foraging behavior. In addition, an arbitrary decision had to be made to distinguish short trips from very long visits when elephants remained close to waterholes.

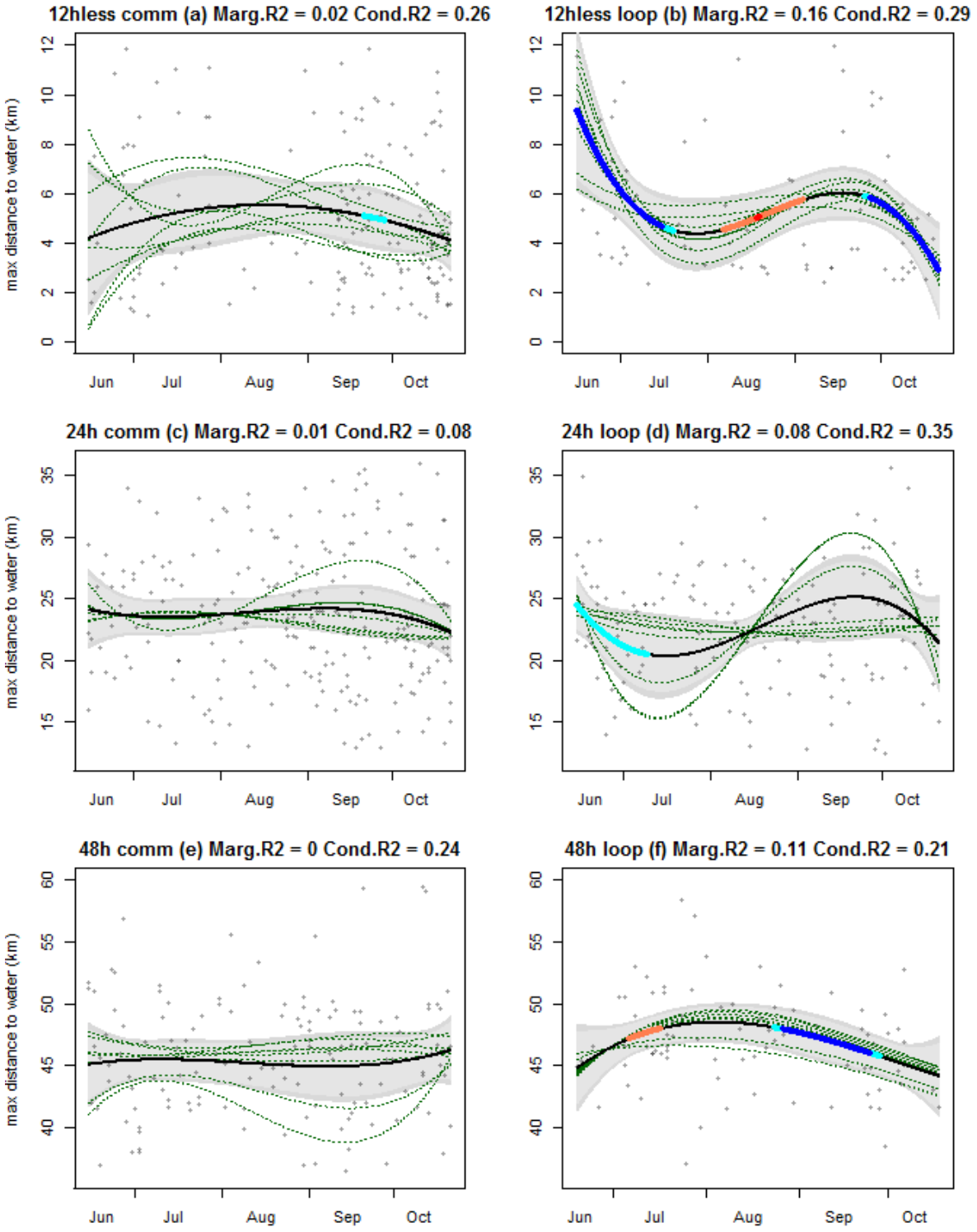


Figure 29: Trip duration throughout the dry season: short trips (a,b), 24h trips (c,d) and 48h trips (e,f). Left panels show commuting trips (a,c,e) and right panels looping trips (b,d,f). The main fixed effect are shown by the back curve with 95% confidence interval in grey. Significant increase are over-plotted in red (95% CI) or orange (90% CI), significant decreases are over-plotted in blue (95%CI) or in cyan (90% CI). Green dashed lines represent individual predictions including the random effects.

7.2 Elephant drinking time

The near circadian periodicity of longer 24h, 48h and 72h foraging trips that account for 95% of elephant's time may result from elephants having a preferred drinking time at dusk. Elephants generally prefer coming to drink during the first hour after sunset. Median arrival time is 18h40 +/- 5h. However, drinking time varied consistently between family groups throughout the dry season.

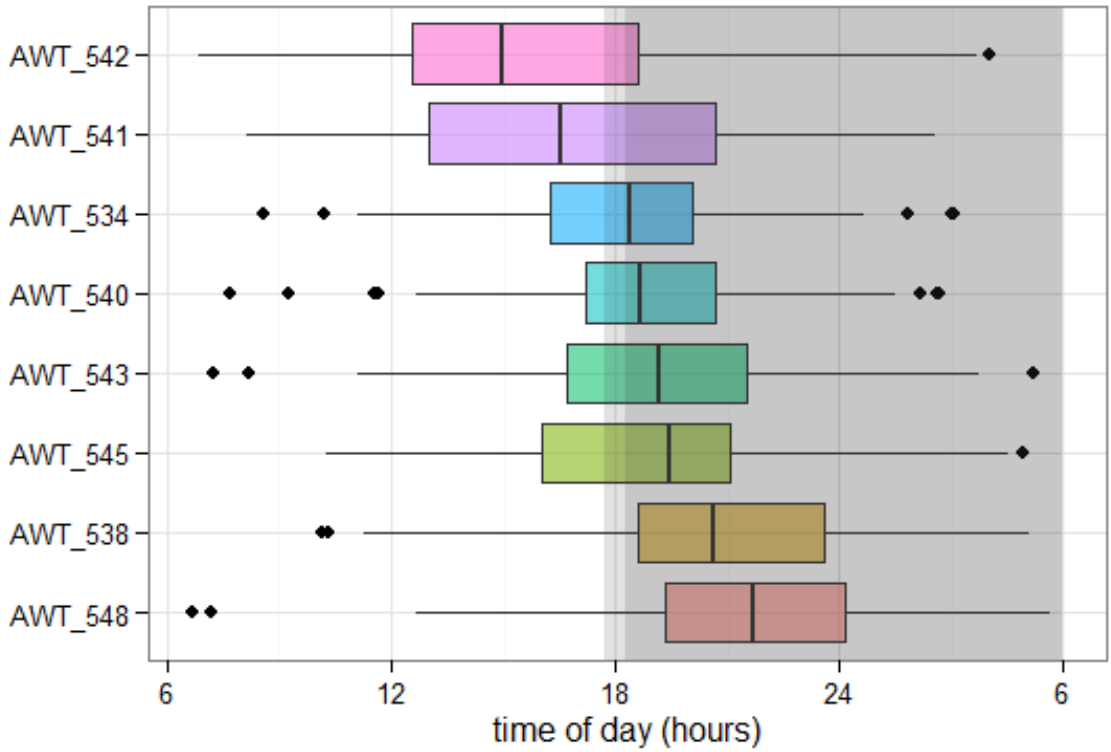


Figure 30: Drinking times of 8 collared elephant groups during the 2013 dry season. Two preferred coming to waterholes 1h (541) or 2h (542) before sunset. Four herds followed the general pattern by arriving just after sunset. Two other groups preferred coming about 3h after sunset (538 & 548).

7.3 Elephants adjust trip duration to drinking time

Elephants appear to modify trip duration to maintain their crepuscular drinking schedule. Following each visit, trip duration is below average if the elephant depart after sunset and above average if the elephant depart before sunset (Figure 31). The next visit therefore occurs closer to sunset. However, except for 72h trips they do not alter trip duration sufficiently to compensate for the offset: for each hour, 12h trips were shortened by 14%, 24h trips by 51%, 48h trips by 38% and 72h trips by 119%. It is therefore more likely that for longer offsets, elephants return to their preferred arrival time by making short trips.

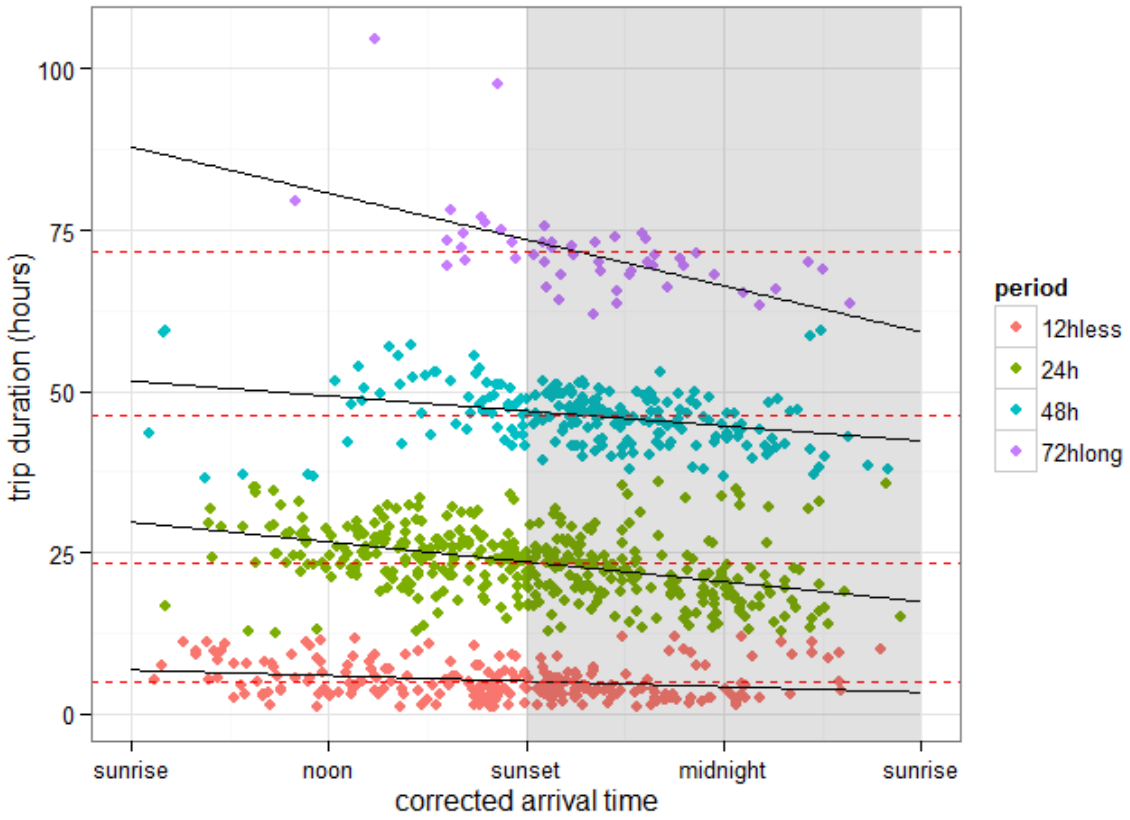


Figure 31: Trip duration decreases with relative arrival time defined as the difference between arrival time and sunset to account for changing day lengths throughout the dry season. Dashed horizontal red lines represent mean trip duration. Trip duration regression lines were modeled using a mixed linear model (lme4 package in R) with trip period, corrected arrival time and their interaction as dependent variables. Random effects by individual included a random intercept and slope of arrival time.

Chapter 3: The further from water the better. Does forage depletion override landscape complementation in elephant's selection of foraging locations?

Hugo Valls Fox, Hervé Fritz, Michel De Garine-Wichatitsky & Simon Chamaillé-Jammes

Abstract

- Landscape complementation occurs when non-substitutable resource patches are sufficiently close to one another for animals to successfully exploit them. However, areas where both resources are close to one another are expected to carry higher consumer densities. As a result, these areas are rapidly depleted and eventually avoided. We predict the spatial distribution non-substitutable resources has opposing effects on consumer habitat selection according to the scale of the investigation: At fine scale habitat, animals avoid patches that are closest to each other due to resource depletion, whereas at large scales, animals select the areas of the landscape that offer the best resource complementation.

- During the dry season, surface water and forage are non-substitutable resources for African elephants. We analyzed GPS relocation data of family herds living in Hwange National Park, Zimbabwe, to test the multiscale effects of waterhole density on elephant habitat selection during foraging trips.

- Contrarily to our expectations elephants avoided areas with high waterhole density at both fine scales (<1km) and large scales (5km-7km). Avoidance appeared to be greater when elephants foraged far away from the waterhole they drink from and this effect appeared to be more marked as the dry season progressed.

- Elephant avoidance of areas with high waterhole densities suggests distance to water alone is not sufficient to quantify the effects of forage depletion. By identifying the scale at which elephants respond to water density we provide a template for management of water provisioning in arid and semi-arid landscapes which accounts for the target's species requirements and mobility.

1 Introduction

The spatial patterns of resource distribution strongly influence how animals use a landscape and ultimately their abundance (Dunning, Danielson & Pulliam 1992). For instance, surface water availability is a key determinant of animal distribution in arid and semi-arid regions (Western 1975; Redfern *et al.* 2003; Leggett 2006a; Ogutu *et al.* 2014) and water dependent herbivore populations are regulated by the area that remains accessible during the dry season (Illius & O'Connor 2000). In African savannas, most large herbivore species can no longer obtain sufficient water from the vegetation they consume during the dry season and surface water then becomes a non-substitutable resource. As a result, they must regularly shuttle between foraging patches and waterholes to drink (Brooks & Harris 2008; Cain, Owen-Smith & Macandza 2012; Chamaillé-Jammes et al. 2013, chapter 2). Landscape complementation occurs when non substitutable resource patches are sufficiently close to one another for animals to successfully exploit them (Dunning, Danielson & Pulliam 1992). At the individual level, animals are expected to prefer landscapes with higher complementation to reduce travelling costs. At the population level, these areas should also harbour higher densities (Choquenot & Ruscoe 2003). For example, dry season elephant densities increase with waterhole density in Hwange National Park, Zimbabwe (Chamaillé-Jammes et al. 2008).

However, greater attractiveness of areas offering better complementation may increase an individual's exposure to predation (Davidson et al. 2013) or competition (Walker et al. 1987). Greater accessibility does not entail higher patch quality, rather the contrary, as foraging patches close to water may be heavily depleted by other herbivores especially at the end the dry season. In the long run, the gradient of use entails long term habitat modifications (Thrash & Derry 2008; Chamaillé-Jammes, Fritz & Madzikanda 2009; Landman *et al.* 2012) resulting in a reduction of woody vegetation cover, that may be particularly detrimental to bulk feeders such as elephant. Herbivore species respond differently to the trade-off between foraging patch accessibility and patch quality. African buffalo select for patches with high resource complementation and remain close to water during the dry season (Cornélis *et al.* 2011; Macandza, Owen-Smith & Cain 2012). Conversely, zebra travel longer distances between water and their grazing grounds presumably to access better patches than the ones found close to water (Brooks & Harris 2008; Macandza, Owen-Smith & Cain 2012) . However, if one considers the different scales of foraging decisions (Bailey et al. 1996), the relative importance of resource complementation versus patch quality may vary considerably between small scale patch selection and the choice of seasonal or even lifetime home-range location. Accordingly, selection of foraging areas is expected to be consistent with landscape complementation at large scales and with patch quality at finer scales.

The issue of scale is central to our understanding of the interaction between landscape properties (Wiens 1989), animal movement patterns (Benhamou 2013) and the ensuing outcome of foraging decisions (Bailey et al. 1996; Owen-Smith, Fryxell & Merrill 2010). For instance, Shrader et al. (2011) report a top-down, scale dependent process: Elephants select

for habitats with their preferred tree species more strongly than for individual trees within each habitat. Similarly, the influence of surface water availability on elephant movement may be scale dependent. At large scale, several studies found a strong selection of areas close to permanent water sources (Cushman, Chase & Griffin 2005; De Beer & Van Aarde 2008; Harris et al. 2008; Shannon et al. 2009; de Knegt et al. 2011) suggesting landscape complementation as the initial driver of elephant habitat use. However, at finer scales elephants appear to avoid areas close to water (de Knegt et al. 2011; Roever et al. 2014) indicating patch quality becomes the determining criterion of their foraging decisions at smaller spatio-temporal scales.

We hypothesized the distribution of surface water affects elephant foraging decisions at multiple scales during the dry season. We conjectured that landscape complementation would lead elephants to select for areas with high waterhole density at a large scale but their search for high patch quality would lead elephants far away from water at smaller spatial scales. We conducted a habitat selection analysis that directly tested for such multiscale effect of waterhole density. The study was based on GPS relocation data of elephant family herds living in Hwange National Park, Zimbabwe. To avoid the confounding the effects of different behavioral states (Roever et al. 2014), we restricted our study foraging locations based on previous analyses of elephant's movement patterns (Chamaillé-Jammes et al. 2013). Unlike previous studies that assumed the effect of waterholes was captured by the distance to the closest water source (De Beer & Van Aarde 2008; Cushman, Chase & Griffin 2010; de Knegt *et al.* 2011; Chamaillé-Jammes *et al.* 2013), we explicitly modelled waterhole density using a Gaussian kernel method that allowed us to compare different spatial scales given by the smoothing factor (Cushman, Chase & Griffin 2010).

2 Methods

2.1 Study area

The study was conducted in the eastern region of Hwange National Park, Zimbabwe. The area is characterized by relatively level terrain (alt. 1000-1100m asl) and the vegetation is typical of dystrophic semi-arid savanna. Mean annual precipitation is c. 600mm with large variations between years (Chamaille-Jammes, Fritz & Murindagomo 2006) The ecology of the Park is highly seasonal, about 80% of the annual rainfall occurs between November and April. Natural depressions and dams fill up with water during the rainy season but gradually dry up throughout the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007a). There are no perennial rivers in the Park, and at the end of the dry season surface water can only be found at artificial waterholes in which groundwater is continuously pumped, in the study area. Water-dependent species such as elephants must undertake foraging trips to and from these waterholes (Chamaillé-Jammes et al. 2013). This creates local forage depletion near waterholes, and on the long-run habitat changes: vegetation cover increases with distance to water up to several kilometers away from these waterholes (Chamaillé-Jammes et al. 2009, unpublished information).

2.2 Surface water availability

The study was conducted during the course of the 2013 dry season. The study began on June 13th when the elephants had settled in their dry season home-range and ended on October 23rd when they dispersed again after the first significant storm. We monitored all natural pans and artificial waterholes over a c. 2000 km2 area. During the course of the study period, the number of pans containing water in the area declined from 105 to 57, however the increase in distance to water was buffered by artificial water pans (Chamaillé-Jammes, Fritz & Murindagomo 2007b). Indeed, the distribution of water pans in the landscape is uneven; the effect of the dry-up of pans close to pumped waterholes is negligible whereas the dry-up of isolated pans implies entire areas may no longer be accessible to herbivores. We identified three breakpoints coinciding with the largest changes in the distribution of distance to water in the study area (Figure 32). The first two periods were during the cold dry season when changes in surface water availability are greatest. The decrease subsequently levels off during the transition period (mid-dry season) and surface water availability remains unchanged during the hot dry season.

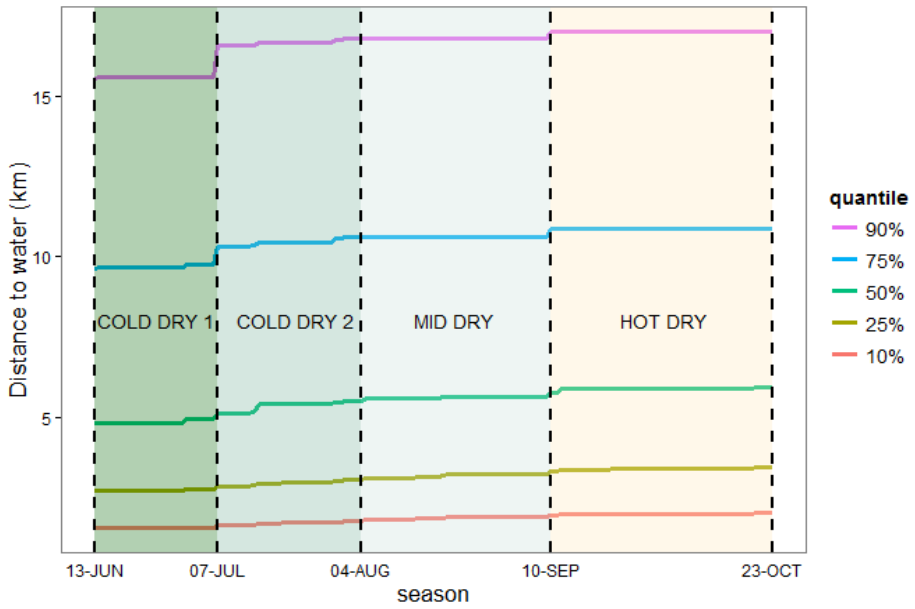


Figure 32: Distance to water during the dry season. Four periods were defined corresponding to increasing distance to water as smaller natural pans dry up within the combined dry season home-ranges of the 8 collared elephants. The cut-off dates were chosen to match the largest changes in surface water distribution.

2.3 Elephant movement data

Movement data was obtained from thirteen adult females belonging to different family herds that had been equipped in November 2012 with GPS collars (Africa Wildlife Tracking). Collars were programmed to record a location every 30 minutes. Visits to waterholes were identified according to the method described in chapter 2. We retained data from 8 collars for which fix

success rates enabled us to reliably identify visits to water. A trip was defined as elephant movement occurring between two consecutive visits to water. We identified 901 trips (chapter 2) of which 62% were looping trips that are characterized by the fact elephants return to the same waterhole they previously drank from.

2.4 Resource selection function of foraging events

Previous studies have shown one cannot ignore behavior to assess foraging habitat selection particularly for African elephants (Roever et al. 2014). Elephant movement during the dry season can be segmented into a succession of trips between waterholes. In Hwange NP, trips last on average 5h, 24h, 48h or 72h (chapter 2). Trips can be categorized as looping or commuting trips: During looping trips elephants return to the same waterhole. Commuting trips are characterized by the fact the trip's end point is a different waterhole (Chamaillé-Jammes et al. 2013). During a typical looping trip, an elephant will head out in a chosen direction, start foraging once it has reached a certain distance from water and finally return to the waterhole to drink. Following this assumption, for each trip we extracted two plausible foraging locations: "Far", The farthest point from the waterhole and "middle", when 50% of trip duration had elapsed (Figure 33). We only included a single point per trip since locations within a trip are highly correlated. However, assumptions concerning foraging locations are inappropriate for commuting trips, especially at the end of the dry season, during which it is unclear where and when elephants feed, and if they have the ability to select for foraging grounds while they travel between waterholes (chapter 2). Thus habitat selection during commuting trips may also depend on higher order selection processes determining the choice of the water pan. We therefore restricted our analyses to looping trips.

2.4.1 Case control design

We followed a case-control approach (Fortin *et al.* 2005; Forester, Im & Rathouz 2009). The analysis was run separately for the datasets of "far" and "middle" foraging points for each season. There were 70 trips during cold dry season 1, 72 trips during cold dry season 2, 95 trips during the mid-dry season and 107 during the hot dry season (Figure 32). Following the case control approach, the data was organized in strata. Each stratum consisted in an estimated foraging location of a trip (far or middle) and its paired controls. Controls were regularly sampled at the same distance from the water pan at which the elephant drank (Figure 33). They were evenly spaced every 500m along the circle centered on the water pan, the number of controls was thus proportional to the circle radius. For the shortest trips, when distance to water was less than 655m, a minimum of 8 points were kept in each cardinal direction (N, NE, E, SE, S, SW, W & NW). Model estimates were qualitatively similar when only 8 random control points were kept for each observation regardless of distance to water.

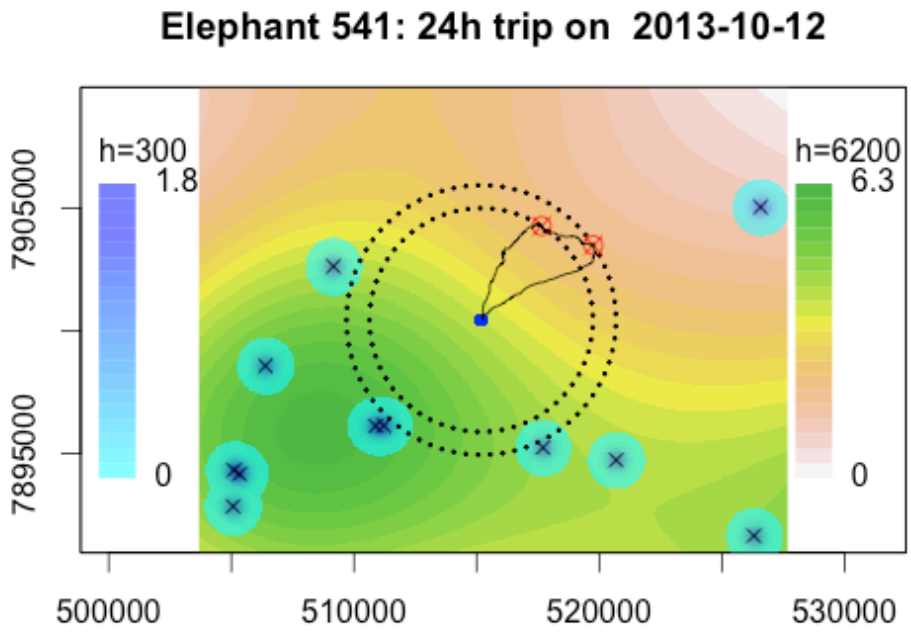


Figure 33: Habitat selection according to waterhole density: For each looping trip (black line) the foraging location is obtained by extracting either the GPS location that is furthest from the waterhole or the one that is in the middle of the trip (red circles). Controls are drawn every 500m along a circle at the same distance to the water pan. As described above, waterhole density was computed at two scales using a small smoothing factor (blue, sd=300m) and a large smoothing factor (green-brown, sd=6200m). Pans included in the waterhole density calculations are marked by by a cross. Note that the water pan at which the elephants drank is not included to avoid correlations with distance to water when the smoothing factor is small. Universal Transversal Mercator (UTM) coordinates are given in meters.

2.4.2 Mapping waterhole density

Elephants essentially use areas comprised between 2 km and 6km from water and seldom travel beyond 10 km from any waterhole during the dry season. A simple measure of landscape accessibility is the distance to the closest water pan. However, locations at the same distance to water may be at widely differing distances from other waterholes. In order to obtain a measure of water pan density, we defined waterhole density (WD) for each control and each observed location $\boldsymbol{x_i}$ as follows:

$$\boldsymbol{WD_h(x_i) = \frac{\sum_{j=1}^{n} G\left(d(x_i, wat_j), \sigma = h\right)}{G(0, \sigma = h)}}$$

Where $\boldsymbol{d(x_i, wat_j)}$ is the distance between waterhole **j** and location $\boldsymbol{x_i}$, **n** the number of pans in the study area still holding water, **G** is the Gaussian density function and its standard deviation equals the smoothing factor **h**. The Gaussian density function was chosen because it decreases monotonously towards zero as distance to water increases. It effectively accounts for the influence of the closest pans while the influence of distant pans is negligible. Waterhole density was normalised for computation purposes, the correction $\boldsymbol{G(0, \sigma = h)}$ does not

create any bias in model estimates. In addition, the normalisation provides biologically meaningful values to waterhole density. As a result, the smoothing factor, **h**, can be considered as the area of influence of a given water pan. One can interpret the waterhole density value as the number of pans within a distance of **h** (Figure 33). When the smoothing factor is small, e.g. h=300m, the area of influence of different waterholes seldom overlap in the waterhole density map. As shown in Figure 33, waterhole density values increase from 0 to 1 around isolated water pans and up to 1.8 for two pairs of pumped water pans only a few hundred meters apart. Conversely, the areas of influence of each water pan overlap extensively when the smoothing factor is large (e.g. h = 6200) creating a gradient from areas with high waterhole density to areas with low waterhole density (Figure 33). Thus, the smoothing factor, h, summarizes the scale at which waterhole density influences elephant habitat selection in subsequent models.

2.4.3 Model selection

In order to model the potentially opposite effects of landscape complementation and patch quality, we developed a habitat selection model that included waterhole density at two different scales:

$$w(x_i)_{dwat_i} = exp\left(\beta_{small} WD_{small}(x_i) + \beta_{large} WD_{large}(x_i)\right) \textit{ two-scale model}$$

Where $w(x_i)$ is the relative probability of selecting a location x_i; β_{small} and β_{large} are the relative selection strengths respectively associated to waterhole density at a fine scale $\boldsymbol{WD}_{small}(x_i)$ and waterhole density at a large scale $WD_{large}(x_i)$. To test the multiscale hypothesis, we compared the fit of this two-scale model with a one-scale model. The one-scale model was specified as follows:

$$w(x_i)_{dwat_i} = exp\left(\beta_h \times WD_h(x_i)\right) \textit{ one-scale model}$$

We used the quasi-likelihood under independence criterion (QIC), designed for case-control models for this comparison (Craiu, Duchesne & Fortin 2008). The fits of both models vary according to the values of the smoothing factor(s). Before comparing these models we determined the smoothing factor(s) that provided the best fit for each model (Appendix I). For each season, the best-fitting two-scale model was then compared with the best-fitting one-scale model (Table 3).

The best one-scale model was obtained by comparing the QIC of models with a smoothing factor (h) between 200m and 12km by 100m increments (Appendix I). The best two-scale model was obtained by testing different pairs of smoothing factors: with a small smoothing factor h_{small} that varied from 200 m to 5 km and with a large smoothing factor h_{large}, that varied between 2.5 km and 12 km (Appendix I), and the constraint that $h_{small} < h_{large} - 1000$. Since the ranges of both smoothing factors overlap, we could not allow both smoothing factors to be too similar.

The relative selection strength indicates whether elephants respond to landscape complementation or patch quality. If the relative selection strength is positive, elephants select for areas with high waterhole density. Conversely, a negative relative selection strength indicates elephants prefer areas with low waterhole density. The model allows for the relative selection strength to vary linearly according to distance from the trip's water pan ($dwat_i$) :

$$\boldsymbol{\beta_h = a_h \times dwat_i + b_h}$$

Second and third degree polynomial functions were also tested but they did not improve model fit.

Table 3: Smoothing factors (h) and QIC values of the best-fitting one-scale and two-scale models. See text for details. Results are presented for each season and for analyses conducted on either the location furthest from water (far) or the location at which 50% of trip duration had elapsed (middle). Models with a lower QIC have more support. ΔQIC is the difference between the QIC of the best model with 1 waterhole density function and the QIC of the best model with 2 waterhole density functions.

		Best one-scale model		*Best two-scale model*			
***F*oraging**	**Season**	**h**	**QIC**	**h small**	**h large**	**QIC**	**ΔQIC**
far	Cold dry 1	1600 m	443	900 m	5900 m	432	11
far	Cold dry2	5300 m	542	400 m	5500 m	532	10
far	Mid dry	7600 m	645	400 m	7600 m	641	4
far	Hot dry	6100 m	728	300 m	6200 m	725	3
middle	Cold dry 1	2200 m	456	700 m	5400 m	443	13
middle	Cold dry2	4300 m	494	400 m	5000 m	478	16
middle	Mid dry	5800 m	625	400 m	6100 m	613	12
middle	Hot dry	6200 m	706	600 m	6400 m	696	10

Model goodness of fit was assessed by k-fold cross validations with 10 bins and 100 iterations (Fortin et al. 2009; Basille 2015) (Figure 34) and the quality of the model estimated as the Spearman rank correlation between observed and predicted data (Boyce et al. 2002). A subsequent t-test was applied to determine whether the correlations for observed locations were greater for the two-scale model than the one-scale model.

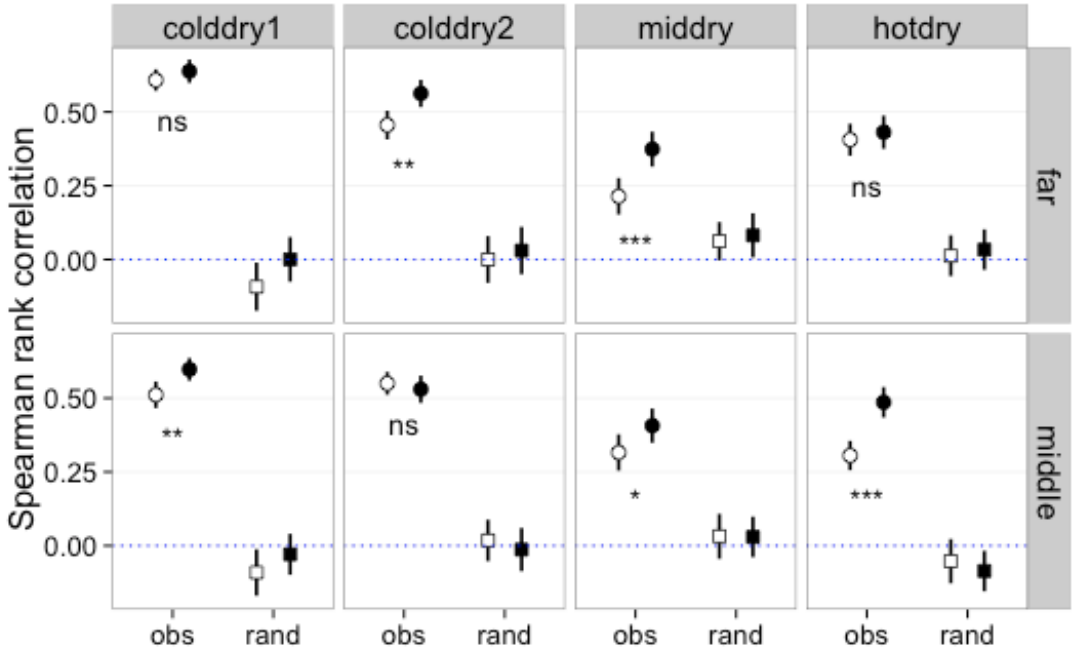


Figure 34: Results of the K-fold cross-validation of the best-fitting one-scale (open symbols) and two-scale (closed symbols) models. Mean Spearman rank correlations and 95% confidence intervals were computed for both observed locations (circles) and random locations (squares). For each season, model validation was done on the furthest foraging locations (top panels), as well as the middle foraging location (bottom panels). Higher Spearman rank correlations indicate a better model prediction. One way Student's t-test comparison of means were used to test if validation scores of two-scale models were greater than those from one-scale models: ***: p<0.001, **:p<0.01,*:p<0.05 and NS: p>0.05.

3 Results

The best-fitting two-scale models predicted observed elephant locations reasonably well (Figure 34), and were always better, based on QIC, than one-scale models (Table 3), thus demonstrating the multi-scale response of elephant foraging to waterhole density. The best-fitting smoothing factors in the two-scale models were fairly consistent for all 4 periods of the dry season and for the two types of locations analysed (far or middle of the trips). The smoothing factor of the large scale waterhole density function ranges from 5km to 7km and the one of the small scale waterhole density function is always less than 1km (Table 3).

Landscape complementation is expected to influence selection at large scales whereas patch quality is expected to affect selection at small scales. However, at the large scale the strength of selection for areas with high waterhole density was almost always negative (Figure 35), demonstrating elephants avoid of these areas during foraging and supporting the patch quality hypothesis rather than the landscape complementation hypothesis. Avoidance appeared to be greater (i.e. selection strength more negative) when elephants foraged far away from the waterhole they drank from (Figure 35), and this effect appeared to be more

marked as the dry season progressed (i.e. the slopes become steeper; Figure 35). Interestingly, the robust standard error extend above zero during the second half of the cold dry season and selection strength of the large scale waterhole density function is actually above zero for the first few kilometres during the mid-dry season. During these periods, short trips could be consistent with the landscape complementation hypothesis since a positive relative selection strength coefficient implies selection for areas with higher waterhole density. However, the positive values of the selection strength for the few first kilometres might be an artefact of the slope/intercept correlation resulting from high leverage effect of the few foraging locations with strongly negative selection strengths beyond 10 km from water (Figure 35). Relative selection strength was no longer positive for the first few kilometres from water when these locations were removed. However, the slope remained unchanged during the hot dry season.

At the small scale, the consistently negative value of the selection showed that elephants strongly avoid entering within the immediate vicinity of water pans during looping trips (Figure 36). The value of the smoothing factor of the small-scale waterhole density function - less than 1 km - implies Gaussian density functions don't overlap unless water pans are within a couple of hundred meters of each other (Figure 33). Because looping trips are defined by the fact elephants do not get within less than 200m of a water pan (Chapter 2), avoidance of areas within a few hundred meters of other water pans is therefore an intrinsic property of the looping trips analysed here. Nonetheless, small scale avoidance of water pans appears stronger when elephants travel further from water during most of the dry season. This is not observed in a few instances (during the hot dry season for the furthest foraging location and for the second half of the cold dry season for the mid-trip foraging location) but in these cases two-scale models did not improve predictions compared to one-scale models (Figure 34) suggesting elephants occasionally foraged close to isolated water pans while avoiding areas with high waterhole density at a large scale.

Overall, the comparisons of two-scale models with one-scale models revealed that the effects of surface water distribution were much more important at the larger than at the smaller scale. Indeed, smoothing factors of the best-fitting one-scale models were generally similar to the ones of the large-scale waterhole density function of the two-scale models (except for the cold dry season 1; Table 1). Moreover, the differences in the predictive ability of two-scale and one-scale models, although often significant, were generally small (Figure 34). Thus, we concluded that two-scale models resembled one-scale models with an additional small-scale avoidance effect of areas with high waterhole density which marginally improved models.

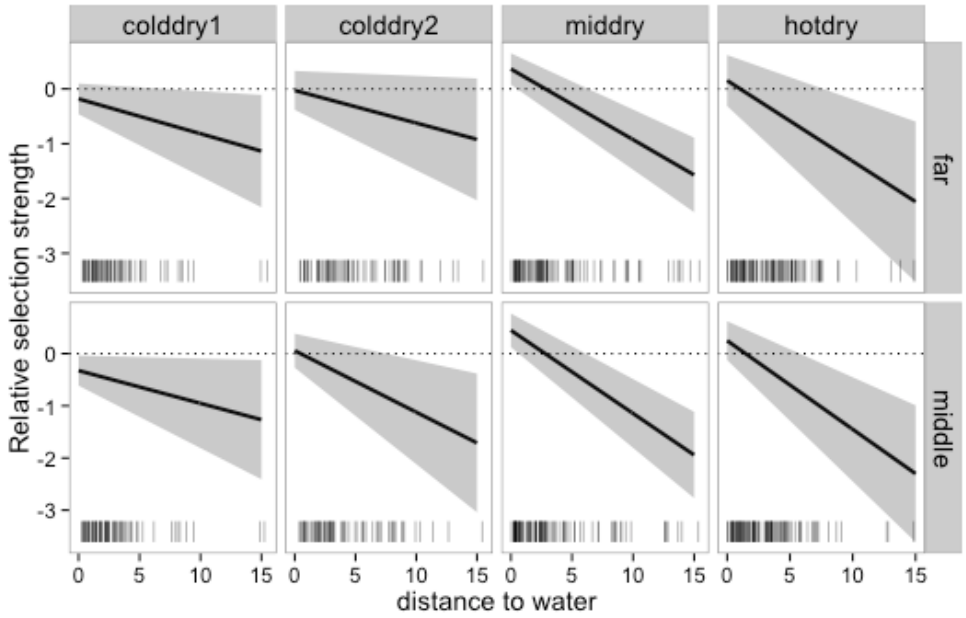


Figure 35: Selection strength of the large scale waterhole density function from the best two-scale model according to distance to water. The best two-scale model was estimated for each season (left to right) for the far (top line) and the middle foraging point (bottom line). Shaded areas represent parameter standard error. The distribution of observed locations according to distance to water is given by the vertical bars at the bottom of each panel.

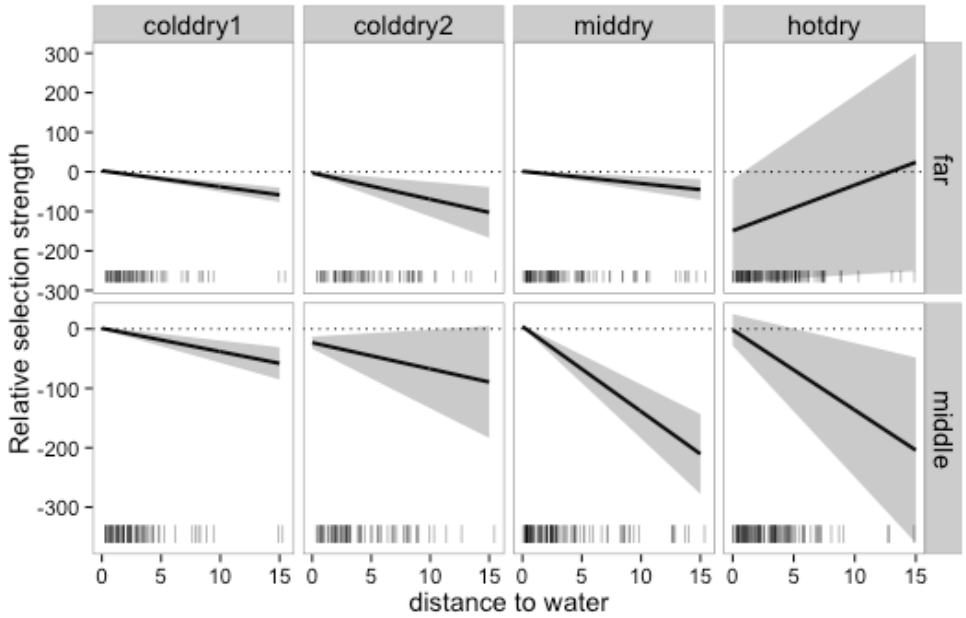


Figure 36: Selection strength of the small scale waterhole density function from the best two-scale model according to distance to water. The best two-scale model was estimated for each season (left to right) for the far (top line) and the middle foraging point (bottom line). Shaded areas represent parameter standard error. The distribution of observed locations according to distance to water is given by the vertical bars at the bottom of each panel.

4 Discussion

4.1 Elephants forage away from water during the dry season

During the dry season, the distribution of surface water has strong implications on elephant foraging decisions. In Hwange NP, elephant breeding herds select for areas with low waterhole density at large scales (Figure 35) and avoid the vicinity of water pans at fine scales (Figure 36). However, large scale waterhole density was more important than small scale waterhole density, particularly during the hot dry season when the latter was no longer significant (Figure 36). As a result, waterhole density may be more important than distance to water to understand elephant's choice of foraging patches. Namely, at the end of the dry season, elephants would prefer foraging close to an isolated water pan than away from water in an area with a high waterhole density. Therefore, distance to water should be considered as a foraging constraint (chapter 2) whereas the effects of waterhole density on landscape composition may be the underlying currency of habitat selection.

The two scales identified by the best models suggest two levels of forage depletion. The smaller smoothing factor (300m-900m, Table 3) indicates elephants avoid the immediate vicinity of water pans. Herbivore impact is greatest within this sacrifice zone (Thrash & Derry 2008; Valeix *et al.* 2011; Landman *et al.* 2012) which provide hardly any foraging opportunities for elephant. During the dry season, elephants spend very little time in these areas (chapter 2) which they cross at high speed to go and drink (Chamaillé-Jammes *et al.* 2013) . The scale of the large smoothing factor (5400m-7600m, Table 3) is similar to elephant's foraging range (chapter 2). At this scale, areas with low waterhole density likely correspond with areas with low elephant densities and thus lower levels of depletion. The increasing slope of relative selection strength during the course of the dry season suggests large scale selection of low waterhole density areas increases as high density areas become more and more depleted.

In a recent study, Polansky *et al.* (2015) identified goal-oriented movement towards water, by elephant, starting up to 50km from water, suggesting elephants have detailed spatial knowledge of waterhole distribution over large scales. Looping trips can also be considered as goal oriented movement to foraging patches and back (chapter 2). Thus, the selection of foraging patches in areas with low waterhole density at two scales may indicate elephants use this spatial knowledge to target less depleted patches.

Various studies of elephant movement patterns have repeatedly found elephants remain within a few 10-15 km of water during the dry season (Harris *et al.* 2008; Loarie, van Aarde & Pimm 2009; Cushman, Chase & Griffin 2010). To our knowledge, only one study has studied the implications of this constraint, namely that elephants may actually select for areas away from water but are forced to return to water regularly to drink (Roever *et al.* 2014). In our study, we used a single location per trip as an indication of where elephants forage. However, during the dry season elephants spend on 17-19 hours a day foraging (Moss, Croze & Lee 2011). Although elephants strive to forage away from water, they must forage on the way

areas to fulfill their energetic needs. However, the surface area close to water is much smaller than away from water. The combined effect of hundreds of elephants travelling to and from water is much greater close to water, even though they target areas away from water. Our study revealed this discrepancy by pointing out elephant selection of areas with low waterhole density during their foraging trips.

4.2 The scale of landscape complementation

The distribution water dependent herbivores is strongly constrained by surface water (Redfern *et al.* 2003; Ogutu *et al.* 2014), in particular, elephants spend most of their time within a few kilometres from water and rarely range beyond 10km from water (Conybeare 1991, Figure 15) suggesting resource complementation is a key factor of elephant space use. Yet, foraging elephants on looping trips select for areas with low waterhole densities at both large and fine scales throughout the dry season. Within their dry season home-range, patch choice at the scale of a single trip appears to be determined by patch quality rather than resource complementation.

The key notion underlying landscape complementation is proximity (Dunning, Danielson & Pulliam 1992), for instance, in Australia, wild pigs living in riverine systems depend on pastures for forage and riverine woodlands for refuge. Population rate of change was greater for pigs using pastures close to riverine systems resulting from increased foraging efficiency (Choquenot & Ruscoe 2003). Similarly, in Bialowieza Forest, Poland, ravens build their nests in coniferous stands but forage in deciduous woodlands and open areas. As a result breeding performance was higher for couples living coniferous stands which were close to large areas of their preferred foraging habitats (Mueller *et al.* 2009). In both of these studies, landscape complementation occurred at the home-range scale and the effects of resource complementation emerge at the population scale rather than at the individual level. However, landscape complementation effects have been found within an animal's individual home-range such as the selection of refuge areas (Hoglander *et al.* 2015). The negative relative selection strength associated with large scale waterhole density suggest landscape complementation between water and foraging resources may only occur at higher order scales such as the location of the seasonal home-range. Accordingly, individuals are expected to have smaller home-ranges in areas with high resource complementation. During the dry season, elephants living in areas with higher waterhole densities have smaller home-ranges (De Beer & Van Aarde 2008). Thus, during the dry season, elephants may only respond to resource complementation at the seasonal home-range scale (Bailey *et al.* 1996; Owen-Smith, Fryxell & Merrill 2010) and be constrained by distance to water at finer scales.

Shrader *et al.* (2011) suggested that elephants make top-down habitat selection decisions selecting areas that contain a higher proportion of preferred habitat at a coarse scale and subsequently making foraging decisions within the chosen area. Accordingly, resource complementation would drive elephant movement at the largest spatial scales particularly in

arid (Loarie, van Aarde & Pimm 2009; Cushman, Chase & Griffin 2010; Wall *et al.* 2013; Bohrer *et al.* 2014) but turn out to become a constraint at finer scales during the dry season (Chamaillé-Jammes *et al.* 2013; Polansky, Kilian & Wittemyer 2015). However, de Knegt *et al.* (2011), report forage characteristics influenced elephant habitat selection at coarser scales in Kruger National Park. These conflicting results may result from the scale of surface water distribution in Kruger NP. As argued by the authors, overall high artificial waterhole density may remove the constraint at larger scales by guaranteeing resource complementation over nearly the entire park. Thus, in Hwange NP, elephants locate their dry season home-range in the only areas that provide water (chapter 2) and cope with the consequences of their aggregation thereafter.

4.3 From resource complementation to resource depletion: central place effects at the landscape scale.

Central place foraging can be seen as an extreme form of landscape complementation resulting from the widespread distribution of one resource (ie. the food supply) as opposed to the sparse distribution of another non-substitutable, key habitat or resource (i.e. the central place). Forage depletion is a common feature resulting from such landscape configurations. It has been described repeatedly for water dependent herbivores (Adler & Hall 2005; Shrader *et al.* 2008; Rozen-Rechels *et al.* 2015) and colonial sea birds (Birt *et al.* 1987; Elliott *et al.* 2009). Ultimately, the density dependent effects of resource depletion limit population size (Gaston, Ydenberg & Smith 2007; Chamaillé-Jammes *et al.* 2008). The greater importance of large scale waterhole density in elephant habitat selection in our study underlines the fact that the combined effect of multiple piospheres on resource depletion might be stronger than the effect of each water pan, except for the sacrifice zone which was accounted for by the small scale waterhole density function.

In arid and semi-arid ecosystems, large herbivore populations are limited by dry season forage (Illius & O'Connor 2000). However, these ecosystems are also characterized by high levels of inter-annual rainfall variability (Chamaillé-Jammes, Fritz & Murindagomo 2007a). Fluctuating rainfall affects herbivores in two ways: Total dry season forage biomass is positively correlated with precipitation and the dry season range of herbivores is determined by surface water availability resulting from total rainfall and the duration of the rainy season. The second effect is buffered by artificial water provisioning (Chamaillé-Jammes, Fritz & Murindagomo 2007b). Population crashes may occur during droughts when both forage quantity and the area accessible to herbivores is limited resulting in forage depletion (Walker *et al.* 1987). However, rather than buffering such population crashes, artificial water provisioning can result in massive die-offs due to greater forage depletion in areas with high waterhole densities (Walker *et al.* 1987; Owen-Smith 1996).

By directly identifying the scale at which waterhole densities influence elephant habitat selection our study could provide a framework to assess the susceptibility of arid rangelands to such die-offs in time of drought. Foraging elephants avoid areas with high waterhole density at a relatively large scale of 5km-7km that we attributed to forage depletion. Our results suggests artificial water provisioning is optimal for elephants at the 5-7km scale in Hwange NP. If waterhole density is greater, elephants will suffer from intraspecific competition and may be susceptible to die-offs. If waterhole density is lesser, some areas will remain inaccessible to elephants and if dry season density dependence occurs, densities will be lower. However, these suggestions only apply to the dry season range. We do not advocate for uniform waterhole provisioning at this scale throughout the park. As defended by Owen-Smith (1996), the current policy of leaving about 40% of the park beyond elephant's reach during the dry season (Chamaillé-Jammes, Fritz & Murindagomo 2007b) maintains a rainy season range elephants can migrate to, allowing vegetation to recover in their dry season range during the rainy season.

5 Appendix I model comparison

This appendix details the comparison between different smoothing factors which was used to identify the best Resource Selection Function summarized by **Table** 3. The best one-scale model was obtained by comparing models with smoothing factors (h) varying between 200m and 12km by 100m increments based on the data set of “far” foraging locations and “middle” foraging locations (Figure 37). The best two-scale model was obtained by testing different pairs of smoothing factors: a small smoothing factor ranging from 200 m to 5 km and a large smoothing factor between 2.5 km and 12 km (Figure 38). Note the range of values for each smoothing factor do not cover the entire range to ensure that the small smoothing factor was indeed smaller and different from the large smoothing factor ($h_{small} < h_{large} - 1000$). The comparison was done for each season for both “far” and “middle” foraging locations.

5.1 One-scale model comparison

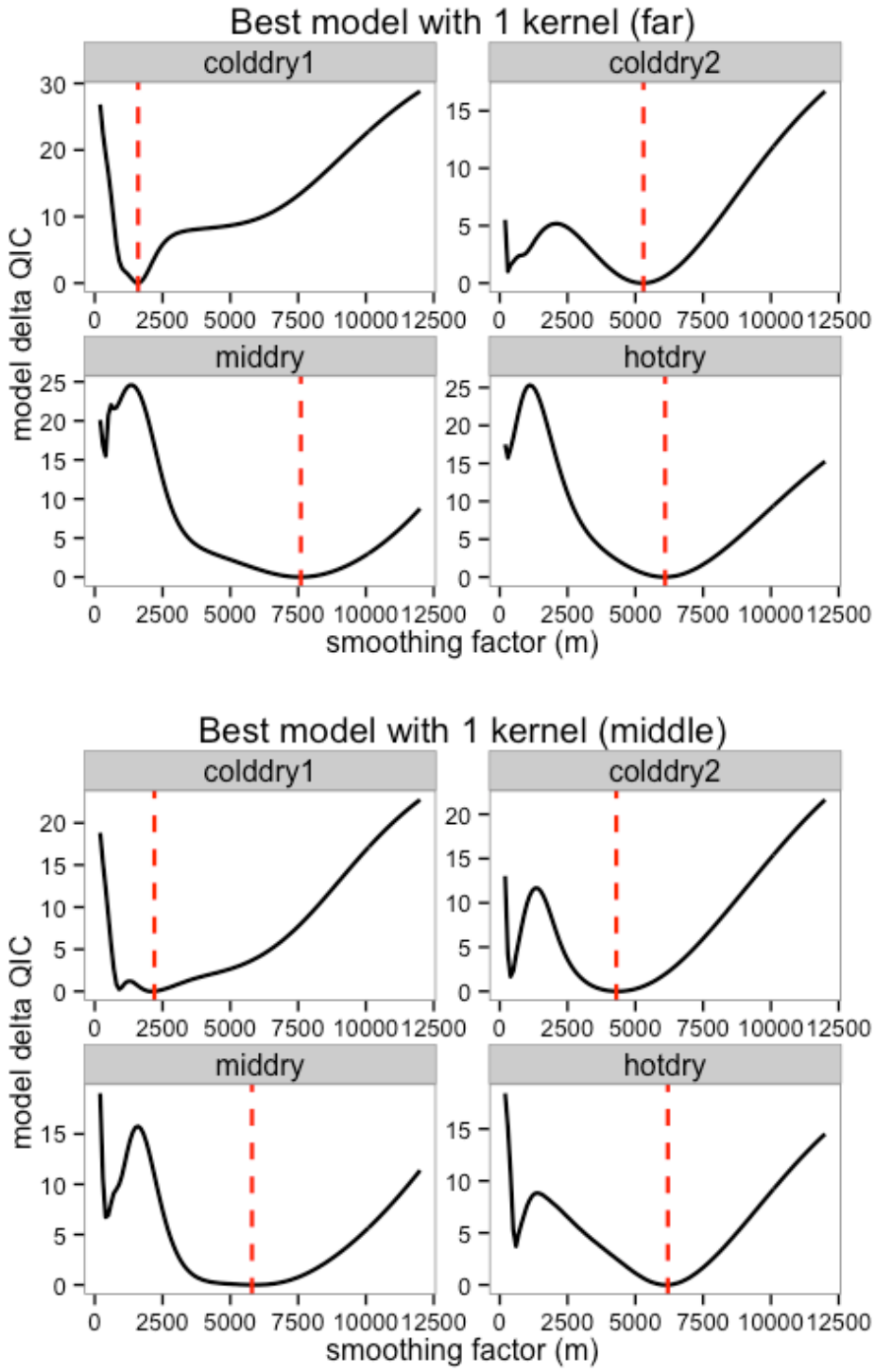


Figure 37 QIC of the one scale models with a range of smoothing factors. The minimum value is shown by the vertical dashed red line.

5.2 Two-scale model comparison

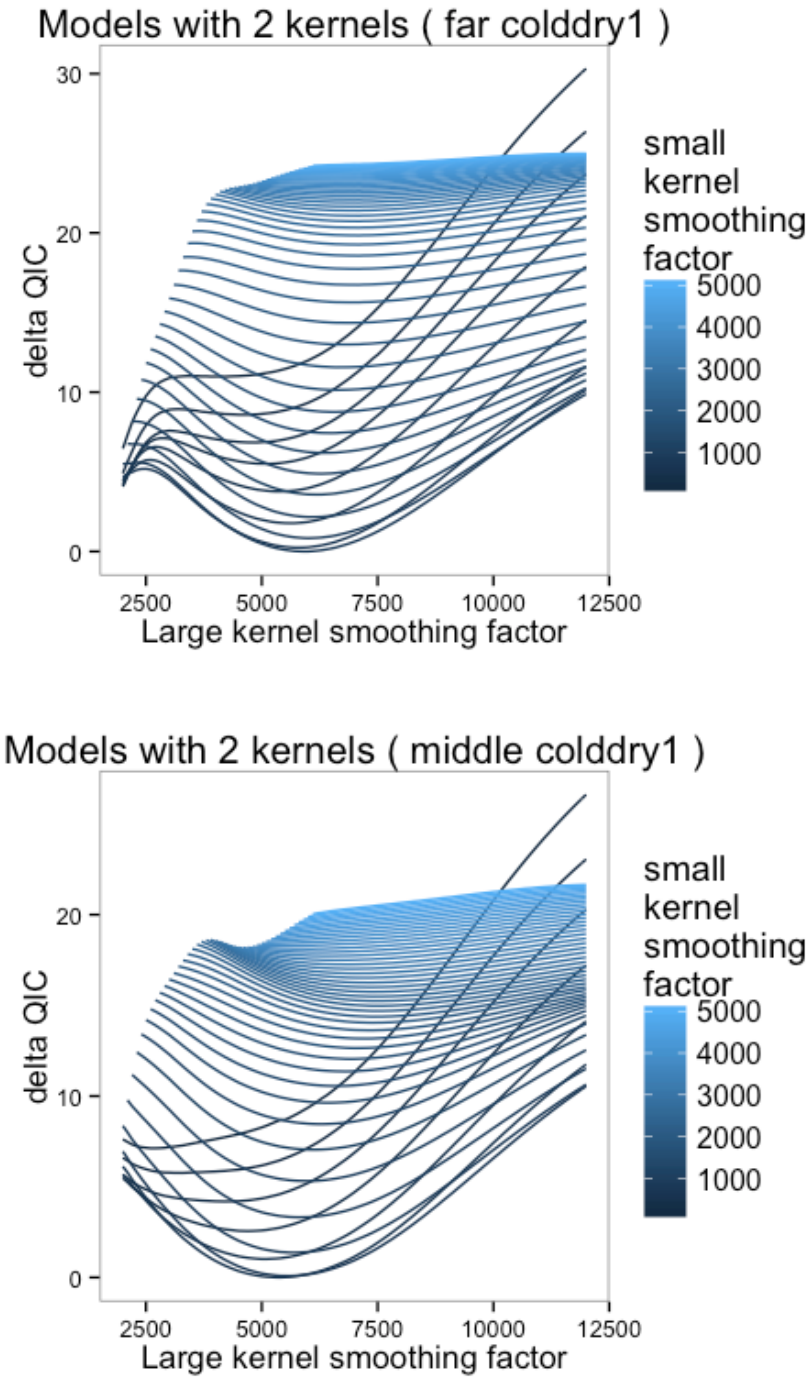
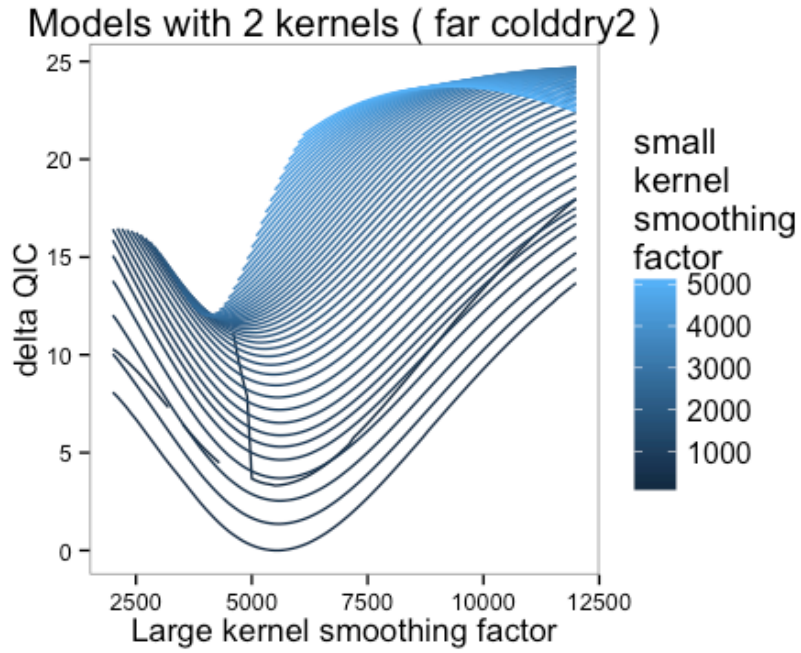


Figure 38: Two-scale model selection. Difference between the QIC of models with different smoothing factors and the QIC of the best model according to the large smoothing factor and the small smoothing factor. QIC values along a same line have the same small smoothing factor.



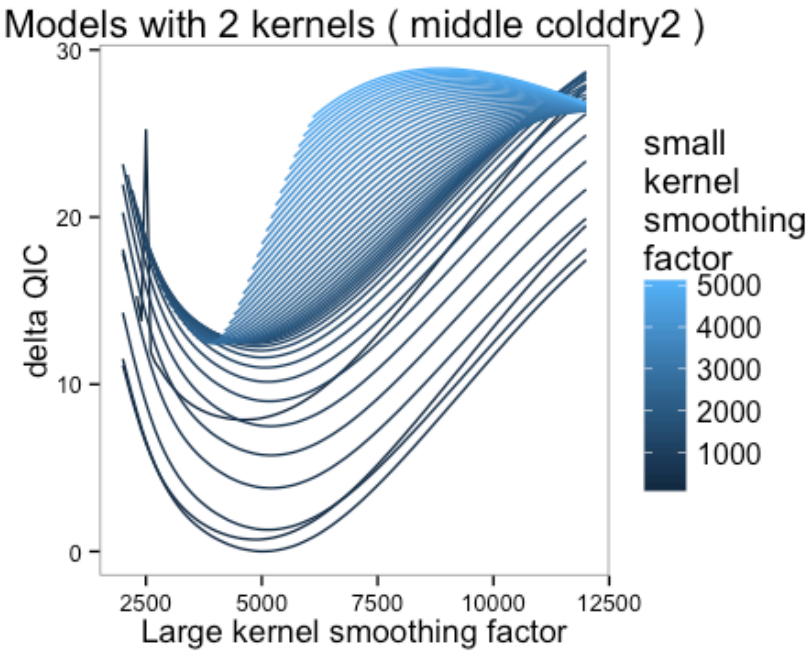


Figure 38 (continued) Difference between the QIC of models with different smoothing factors and the QIC of the best model according to the large smoothing factor and the small smoothing factor. QIC values along a same line have the same small smoothing factor.

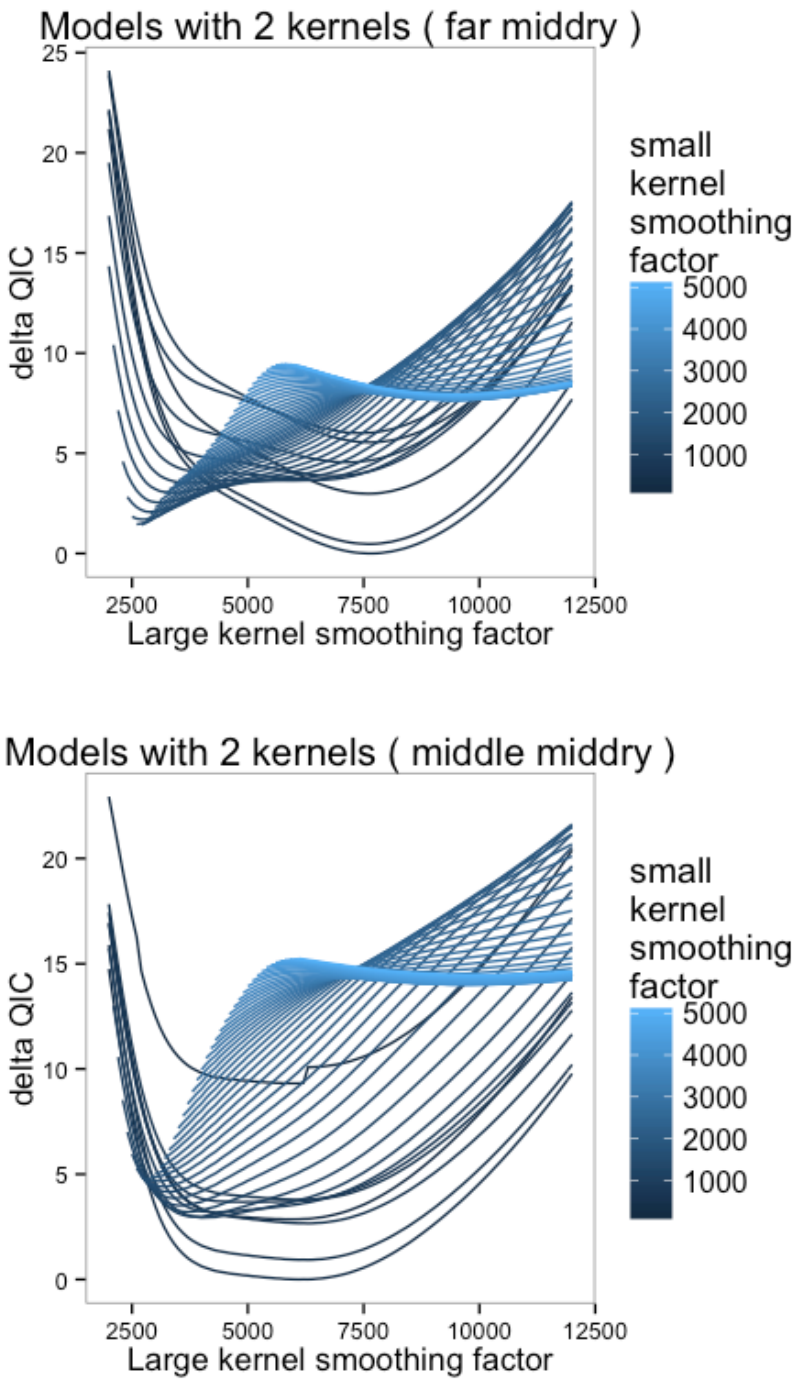


Figure 38 (continued) Difference between the QIC of models with different smoothing factors and the QIC of the best model according to the large smoothing factor and the small smoothing factor. QIC values along a same line have the same small smoothing factor.

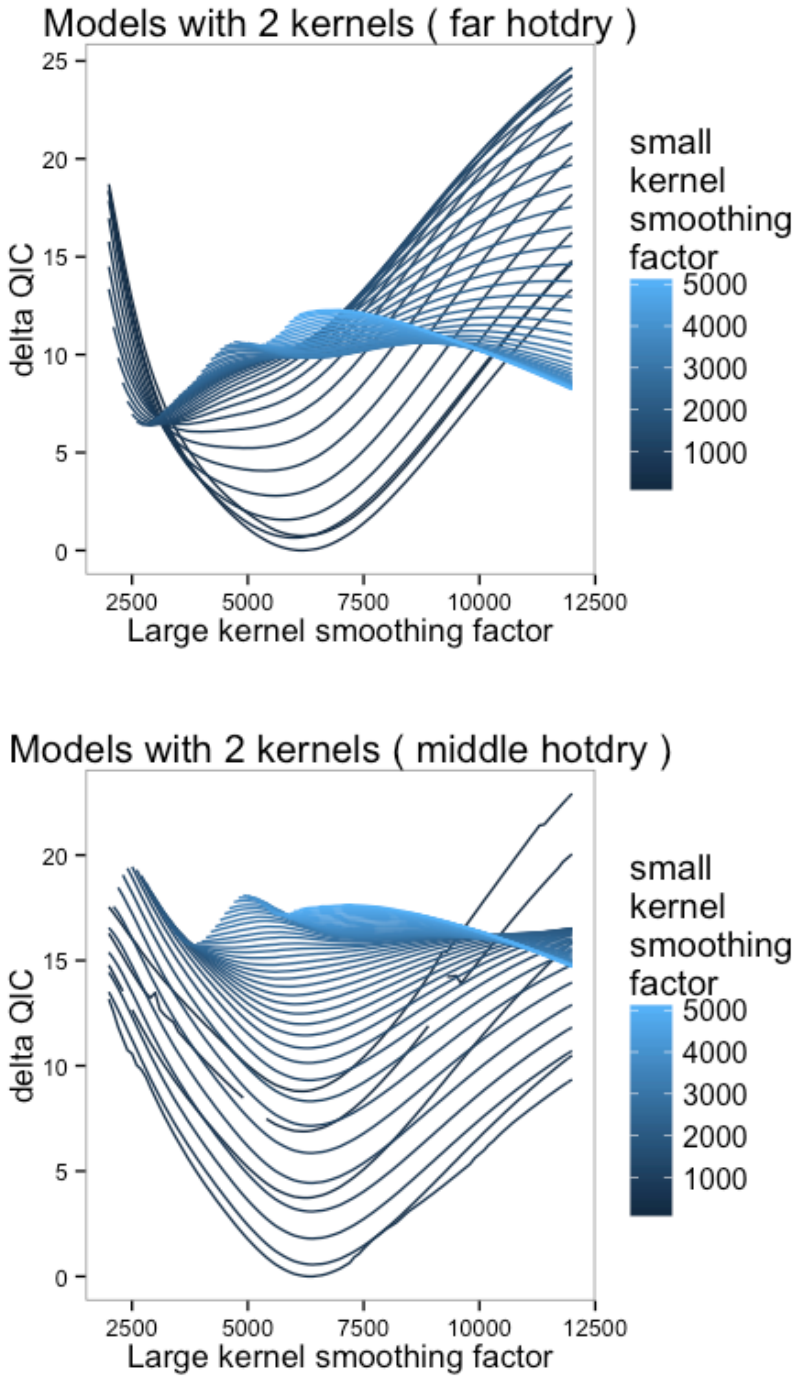


Figure 38 (continued) Difference between the QIC of models with different smoothing factors and the QIC of the best model according to the large smoothing factor and the small smoothing factor. QIC values along a same line have the same small smoothing factor.

Chapter 4: Please keep your distance
Does surface water availability shape the human-wildlife interface at the edge of a protected area?

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In preparation for the Journal of Applied Ecology.

Figure 39: Collared cattle exiting Sikumi Forest during the dry season, elephant bull and buffalo herd about to cross the road cutting across Sikumi.

Abstract

1. Spatial and temporal partitioning of key resources promotes species coexistence. On the edge of unfenced protected areas, livestock and wild herbivores share foraging and watering resources. Can effective resource partitioning be maintained in African savannas as surface water availability declines during the dry season?
2. We quantified avoidance between African elephant, African buffalo and cattle at multiple scales using habitat selection models with GPS relocation data according to seasonal changes in surface water distribution on the eastern fringe of Hwange National Park, Zimbabwe.
3. The range and duration of cattle incursions into the protected area varied seasonally by shifting from consistent selection of open habitats close to water pans during the rainy season to the less predictable selection of areas far away from the now dried up water pans at the end of the dry season.
4. During the rainy and cold dry season, buffalo successfully avoid cattle at large (overlap<3%) and fine spatial scales. By the end of the dry season, buffalo herds, which are restricted to the vicinity of water, still avoid the boundary of the protected area but tolerate higher overlap with cattle (10%) and do not avoid them as strongly at fine scales.
5. Elephant home-ranges overlap extensively with cattle (15-68%) throughout the year but elephant avoid cattle by staying away from the boundary during the day and getting closer to it at night. As the dry season advances, elephant bulls range closer to the boundary especially at night and may even make excursions into the communal land in their search of forage.
6. ***Synthesis and applications****:* Wild herbivores strongly avoid livestock and people at the boundary of a protected area as long as their foraging and drinking resources allow. In the advent of a drought, artificial water provisioning and cattle husbandry determine the level of avoidance and may be used to mitigate disease transmission and crop-raiding.

1 Introduction

Over the past century, human activities have become the main driver of ecosystems worldwide (Ellis & Ramankutty 2008). For instance, artificial water provisioning has led the sedentarisation of previously migratory, or highly mobile, populations of wild herbivores (Davison 1967) and the expansion of livestock husbandry in formerly waterless semi-arid and arid rangelands (Western 1975; James *et al.* 1999). In Africa, the distribution of many large mammalian species is now restricted to protected areas (Blanc *et al.* 2007; Newmark 2008) following their extirpation from other areas (Vandewalle & Alexander 2014) and subsequent land use intensification (Newmark 2008). In addition, anthropogenic barriers have caused dramatic decline in migratory populations by cutting off access to key resources, as has been described repeatedly for wildebeest that suffered massive die offs in times of drought (Spinage 1992). In Southern Africa, fences have been historically erected to separate cattle from wildlife, deemed a reservoir of livestock diseases (Ferguson & Hanks 2010). Fences are also extensively used to delimit conservation areas by keeping wildlife inside and humans out (Hayward & Kerley 2009; Slotow 2012). However, many wildlife areas remain unfenced and current conservation policies in Southern Africa, such as the ones implemented by trans-frontier conservation areas (TFCAs), attempt to restore wildlife corridors between the protected areas, which may imply the dismantling of existing fences (Ferguson & Hanks 2010; Cumming *et al.* 2015). It is therefore essential to improve our understanding of resource use by wildlife on the edge of fenceless protected areas to overcome challenges such as disease transmission (Cooper *et al.* 2010; Miguel *et al.* 2013), crop-raiding (Hedges & Gunaryadi 2010; King, Douglas-Hamilton & Vollrath 2011; Guerbois, Chapanda & Fritz 2012) or livestock depredation (Kuiper *et al.* 2015).

Despite increasing population densities and encroachment by agriculture (Newmark 2008), livestock husbandry and subsistence agro-pastoralism remain the main land-use around wildlife areas in semi-arid rangeland ecosystems and particularly in African savannas (Olff & Hopcraft 2008). Livestock and wildlife ranges may overlap when wildlife is present outside of protected areas (De Leeuw *et al.* 2001; Sitters *et al.* 2009), when they make temporary excursions outside of these areas (Miguel *et al.* 2013) or when cattle make incursions inside protected areas (Hibert *et al.* 2010; Butt 2011; Miguel *et al.* 2013). Livestock and wild herbivore resource requirements overlap extensively (Prins 2000). Resource distribution has been identified as one of key drivers of the spatial distribution of wild and domestic herbivores, particularly incursions and excursions in times of scarcity (Butt 2011; Miguel *et al.* 2013). In this study, we attempt to identify the role of the distribution of surface water, a key resource, on the interactions between cattle (*Bos taurus*) and two large herbivore species, the African elephant (*Loxodonta Africana*) and the African buffalo (*Syncerus caffer*), at the edge of a protected area in North-Western Zimbabwe (Figure 40).

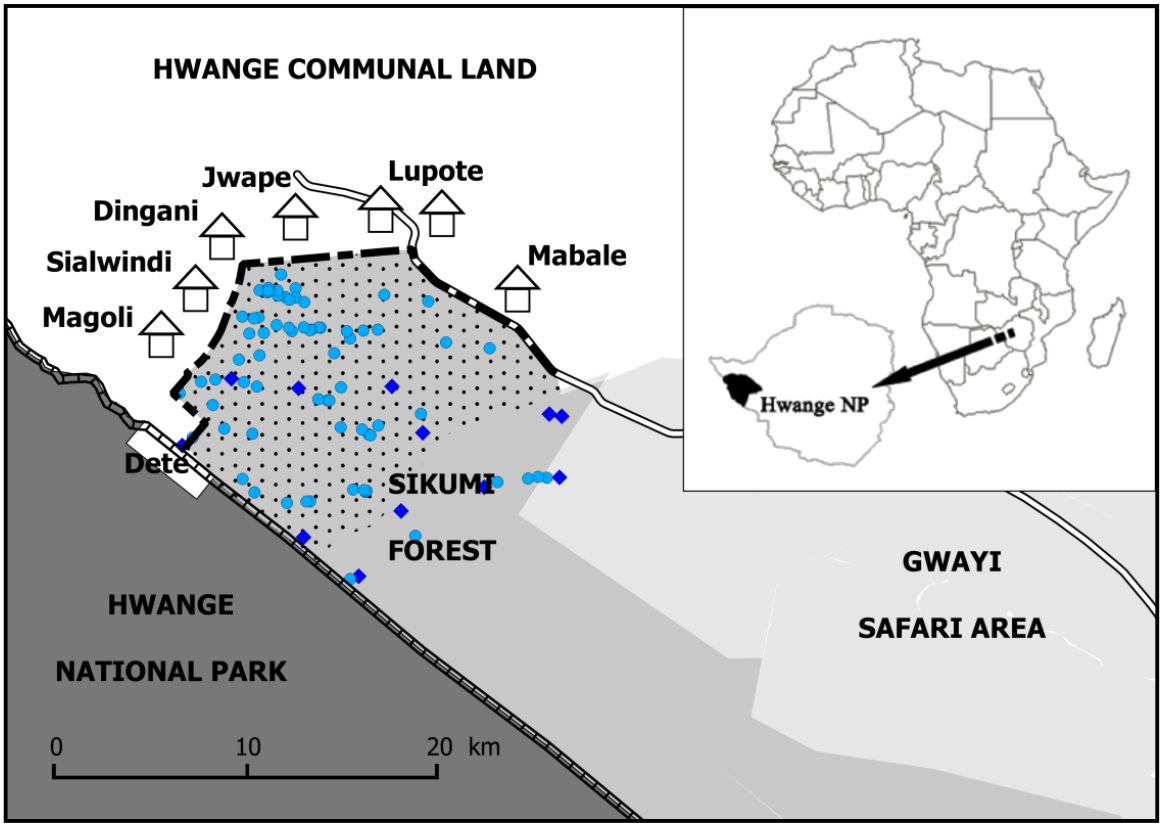


Figure 40: Sikumi Forest study area (190 km^2 dotted area) covers the northern section of Sikumi Forest. Grey areas are designated as wildlife areas where farming is prohibited. Hwange National Park and Sikumi Forest are both dedicated to conservation and photographic tourism, they are separated by a railway line. Gwayi Safari Area is dedicated to trophy hunting on privately owned but unfenced blocks. To the North and East lies Hwange Communal Land (white on map), which consists in dispersed homesteads in a matrix of fields and communal grazing land. Villages along the unfenced border of Sikumi Forest are named on the map. This 30km boundary is represented by a thick dashed line. 10 artificial waterholes (dark blue diamonds) and 78 natural pans (light blue circles) were monitored throughout the dry season during two consecutive years: 2013 and 2014.

Surface water availability is one of the major drivers of arid and semi-arid rangeland ecosystems (Thrash & Derry 2008). Overall, water dependent wild and domestic large herbivores respond similarly to changes in surface water and forage distribution. Herbivores aggregate within a few kilometers of water (De Leeuw *et al.* 2001; Adriansen & Nielsen 2002; Redfern *et al.* 2003; Ogutu *et al.* 2014). At large scales, pastoralists and migratory herbivores contract their range to areas where water persists during the dry season and seek out the best foraging grounds during the rainy season when surface water is no longer limiting (Adriansen & Nielsen 2002; Cornélis *et al.* 2011; Wall *et al.* 2013). At smaller scales, the distribution of water creates central place effects (Chapter 2) as herbivores shuttle between water points and their preferred foraging grounds (Adriansen & Nielsen 2002; Brooks & Harris 2008; Butt 2010; Chamaillé-Jammes *et al.* 2013). As a result, forage depletion will be strongest close to

water and herbivores will range further away from water as the dry season advances (chapter2) (Hunter 1996). In the case of herded domestic herbivores, the central place effects are similar although they are centered on the home kraal rather than water points. However, kraals are often located close to natural water sources or boreholes (Butt 2010, pers. obs.). Surface water also has indirect effects associated with high herbivore densities close to water. Repeated grazing and trampling creates a piosphere (Lange 1969) characterized by the establishment of a gradient in vegetation cover as distance to water increases (Thrash & Derry 2008; Chamaillé-Jammes, Fritz & Madzikanda 2009). Waterholes also attract predators (Valeix *et al.* 2010), increase encounter and mortality risk (Davidson *et al.* 2013; Courbin *et al.* 2015) and ultimately drive the lion-prey spatial game (Courbin *et al.* 2015).

Thus, avoidance between domestic and wild herbivores may result from the balance between each species' own resource requirements and the effects of exploitation or interference competition. For instance, in the Mara-Serengeti ecosystem in East Africa, the degree of overlap between wild and domestic herbivores depends on multiple factors including diet, grazers are generally more water dependent than browsers, and rainfall, herbivores often range further from water during droughts (Ogutu *et al.* 2014). In addition to biotic and abiotic factors, cattle herding practices largely determine these patterns. When cattle are kept close to water, they generally exclude other herbivores (De Leeuw *et al.* 2001; Ogutu *et al.* 2014) conversely when cattle are herded away from natural water sources, wild herbivores distribute themselves more freely (Western 1975; Sitters *et al.* 2009).

Interference competition for access to water between livestock and wildlife could either result in spatial segregation or temporal niche shift (Valeix, Chamaillé-Jammes & Fritz 2007; Crosmary *et al.* 2012b). However, cattle are only present during the day whereas both elephants and buffalo are predominantly crepuscular drinkers even when cattle are absent (Valeix *et al.* 2007, chapter 2) rendering niche shift unnecessary for these species. Segregation between cattle and wildlife may also result from competition for forage. Evidence for exploitation competition is scarce (Prins 2000) since it cannot be inferred from spatial segregation or overlap without measuring its effects on intake. We hypothesized exploitation competition may occur throughout the year for buffalo and cattle that are both grazers whereas it is more likely to be limited to the rainy season for elephant that essentially browse during the dry season (Williamson 1975a). Exploitation competition is expected to be strongest during the dry season when forage is limiting and may be negligible or even outweighed by facilitation during the rainy season (Odadi *et al.* 2011). However, competition may be asymmetrical: Cattle have been reported to compensate for forage depletion by wildlife whereas wild herbivores do not (Young, Palmer & Gadd 2005) moreover standing herbaceous biomass was substantially lower around pans used by cattle than around pans used by wildlife (pers. obs.). As a result, buffalo are expected to strongly avoid areas heavily grazed upon by cattle, especially during the dry season when there isn't any vegetation regrowth.

In addition to responding directly to cattle presence or their effect on foraging resources, elephant and buffalo might also be avoiding human disturbance associated with herding and natural resources collection (e.g. firewood, thatching grass, medicinal plants, animals) (Perrotton 2015). Avoidance of people and anthropogenic features by wildlife is common (Courbin *et al.* 2009; Graham *et al.* 2009; Okello 2010; Leblond, Dussault & Ouellet 2013) and may result in adjustments both in space (Fortin *et al.* 2013) and in time (Crosmary *et al.* 2012b). Unlike the effects of forage depletion, disturbance by cattle and humans may vary widely at two distinct time scales: within a 24h cycle they are present during the day but absent during the night, over a yearly cycle, cattle use different areas according to changing forage and surface water availability. Buffalo and elephant might fine-tune their spatial behavior in response to the spatio-temporal variations of cattle and people presence around waterholes.

Rather than attempting to tease the mechanisms of competition and disturbance apart, we acknowledge both mechanisms may play a key role in the movement patterns of all three species at the boundary of a protected area. As suggested by Miguel *et al.* (2013), surface water availability, and particularly scarcity during the dry season, might be the primary underlying force allowing for spatio-temporal avoidance or overlap.

2 Methods

2.1 Study area

We conducted the study in the ca. 190 km^2 North-Western section of Sikumi Forest, (26.9°E, 18.6°S, Figure 40) located on the North-Eastern boundary of Hwange National Park, Zimbabwe. The unfenced area, which is dedicated to photographic safari tourism, is separated from Hwange National Park by a railway line. There is currently no fence between the Sikumi Forest and the Communal Land to the West, North and North-East (Figure 40). A 30km veterinary fence had been erected in the 1960's, gates were installed along the fence after the 1992 drought to allow cattle to enter, the fence rapidly became ineffective due to lack of maintenance and was finally completely dismantled after the year 2000 by anti-poaching units to remove the wires that could be used for snares. The exact distance cattle are allowed to enter is unclear and remains a bone of contention between local actors (Perrotton 2015). To the West, Sikumi is separated from the villages of Magoli, Sialwindi and Dingani by a secondary tar road. Homesteads and fields are located immediately across the road. To the North, between Jwape and Lupote, the boundary consists in a seldom used track along the old fence poles. The area just north of the boundary is used for crops or grazing grounds, homesteads are located a few hundred meters beyond. The North-Eastern boundary, from Lupote to Mabale and beyond is delimited by the main road between Bulawayo and Victoria-Falls which sustains substantial motor traffic.

Mean annual precipitation is 600mm with large variations between years (Chamaille-Jammes, Fritz & Murindagomo 2006). Climate is characterized by a rainy season that extends from November to April followed by the dry season which can be subdivided in a cold dry season (May-August) and a hot dry season (September - November). There are no perennial rivers in the study area, natural depressions and dams fill up with water during the rainy season but gradually dry up throughout the dry season. By the end of the dry season, surface water can only be found at 11 artificial waterholes in which groundwater is continuously pumped by Forestry managers. Surface water availability for each season was determined following the systematic monitoring of 88 water pans in the area throughout the 2013 and 2014 dry seasons. During the rainy season, 50% of the study area is within 1km of water and the maximum distance to water is 3.3 km.

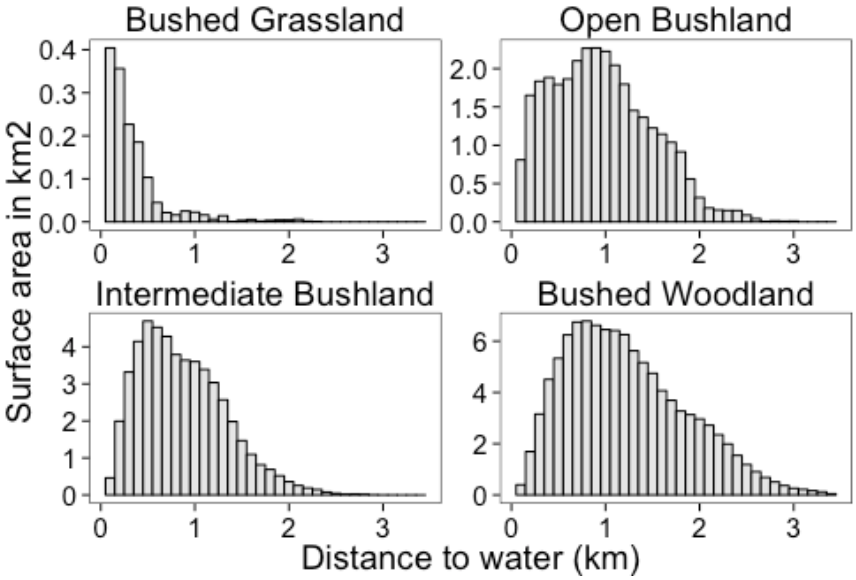


Figure 41: Surface areas of four vegetation classes according to distance to water.

Vegetation is typical of dystrophic semi-arid savanna dominated by the trees *Baikiaea plurijuga*, *Colophospermum mopane*, *Kirkia acuminata* and *Bauhinia petersiana*. Herbivore aggregations around water pans creates piospheres due to repeated grazing and trampling (Lange 1969). Vegetation in Sikumi is similar to Hwange National Park, despite substantial variability in species composition and vegetation structure, woody cover generally increases with distance from water pans (Chamaillé-Jammes, Fritz & Madzikanda 2009). A simplified vegetation map was adapted from (Courbin *et al.* 2015). Four classes were defined according to the proportion of woody cover: Open Grasslands (1.5 km^2) only found within 500m of water pans, Bushed Grasslands (31.5 km^2) and Bushland (51 km^2) both found within 2km of water and Bushed Woodland (106 km^2) that predominantly occupies the areas farthest from water (Figure 41). The vegetation in the Communal Area is similar in composition to the forestry area, however tree cover is much reduced. Upon visual inspection, the open grassland habitat class (Courbin *et al.* 2015) appeared to be congruent with fields in the Communal Lands. We estimate fields occupy about 43% of the land within 2km of Sikumi Forest boundary.

The most abundant herbivore species found in Sikumi Forest are African elephant *(Loxodonta africana)*, African buffalo *(Syncerus caffer),* impala *(Aepyceros melampus)*, greater kudu *(Tragelaphus strepsiceros)* and warthog *(Phacochoerus africanus)*. Large carnivore species include lion *(Panthera leo),* hyena *(Crocuta crocuta),* leopard (*Panthera pardus*), African wild dog *(Lycaon pictus)* and cheetah *(Acinonyx jubatus).*

2.2 Modeling cattle incursions

The following description was obtained by conducting interviews with cattle owners we worked with (n=11) in order to characterize cattle herding practices (Perrotton & Valls Fox unpublished data). Cattle are kept overnight in the family kraal, generally located in close proximity to the homestead to protect livestock from predators. During the study period, 321 kraals were recorded within a 2km buffer along the 30km boundary (Loveridge et al. unpublished data). Although a few households own up to 25 cattle, most kraals only house a few cattle (mean = 5.5) (Perrotton 2015). Thus up to 1700-1800 cattle may be entering Sikumi Forest on a daily basis.

The calendar of cattle incursions in Sikumi can be subdivided into three seasons that are largely determined by agricultural practices (also see Scoones 1995): During the rainy season, along with pastures and drinking water, Sikumi offers the possibility for cattle owners to avoid having their crops being damaged by livestock (Murwira *et al.* 2013; Perrotton 2015). Herd boys drive their livestock to graze and drink into Sikumi nearly every day from November, when the first crops are sown, to early May, once the harvests are over. During the cold dry season, cattle are no longer herded and roam in the villages freely, feeding on grasses in communal pastures and crops residues left in the fields. Some cattle owners store crops residues to feed their animals and keep them from going alone to Sikumi. Even though they graze on communal land, some herds are briefly driven into Sikumi to drink as long as the pans close to the boundary retain good drinking water. Most do not enter Sikumi and drink at boreholes equipped with manual pumps and troughs that provide water for households inside the communal area. During the hot dry season, from August onwards, cattle start returning to the forest to graze on their own. Herders only enter to collect them in the late afternoon, from further and further as the dry season progresses (Valls Fox & Perrotton unpublished interviews).

In agreement with cattle owners, traditional authorities and local veterinary services, cattle belonging to different herds from 6 villages found along Sikumi Forest boundary were equipped with GPS collars recording 1 location every hour (Africa Wildlife Tracking, SA). Five cattle were tracked in 2010-2011 and 9 in 2012-2014. For each one of the three seasons defined by the pastoral calendar, we modeled the probability of cattle presence inside Sikumi Forest with an Inhomogenous Point Process (IPP, that allows making Resource Selection Function inferences) and GPS locations (Johnson, Hooten & Kuhn 2013). IPPs were estimated using Generalized Linear Mixed Models with a logarithm link and a Poisson distribution for

errors, using the lme4 package in R (Bates *et al.* 2015). The model includes a random intercept and slope by individual for the *distance to the boundary* to account for spatial heterogeneity along the border experienced by cattle entering Sikumi Forest at different locations (Gillies *et al.* 2006).

The cattle spatial distribution accounted for *distance to the home kraal*, *distance to the boundary* of Sikumi forest, *distance to water* and *vegetation type (Bushed woodland was used as a reference category)*. Distance to water was based on the rainy season distribution of water pans (Figure 40) for all three seasons because cattle drank at boreholes outside of Sikumi Forest during the dry season but distance to water could account for piospheres effects. To account for non-linear patterns the model also includes the squared distance variables (*kraal, boundary and water*). Central place effects are modeled by the interactions between *distance to the home kraal* with *vegetation type* and *distance to water*, respectively, as well as the *kraal-boundary distance.* The *distance to water x vegetation type* interaction allowed relative selection strength for different habitats to vary according to distance to water.

The aim of the model was to obtain the best fit in order to predict cattle distribution in Sikumi for elephant and buffalo habitat selection models. We proceeded to simplify the model to obtain a better fit for each season using Akaike Information Criterion (AIC). The full model had the lowest AIC during the rainy season. Accordingly, the *kraal-boundary distance* and *distance to water x vegetation type* interaction were removed for the cold dry and hot dry season models. Finally the quadratic effect of the *distance to the home kraal* was removed from the hot dry season model. Model robustness was validated using a 6 fold cross-validation by estimating the model after removing the data from each one of the villages successively (Boyce *et al.* 2002).

The top-ranked model predictions were used to estimate cattle use intensity over the entire study area (30-m resolution grid) for each season. To do so, IPPs were predicted for 321 kraals found within a 2km buffer along the 30km boundary (Loveridge et al. unpublished data). Predicted values were then scaled and summed for each season: The area used by cattle was defined by drawing the 95th percentile of the summed utilization distribution.

2.3 Modeling buffalo habitat selection

Four buffalo cows were collared in November 2012, and their collars transmitted data until September 2013, March, April and August 2014 respectively. A last collar was fitted in December 2013 and provided data until July 2014. Buffalo collars were manufactured by Africa Wildlife Tracking, Pretoria, South Africa (n= 2) and Vectronic Aerospace, Berlin, Germany (n=3). They were scheduled to record 1 location every hour. Collared buffalo belong to a single Buffalo herd of about 500 individuals that occupies our study area in North-Western part of Sikumi Forestry area (Miguel *et al.* 2013). The Buffalo herd is sedentary but exhibits typical fusion-fission dynamics (Cross, Lloyd-Smith & Getz 2005). Over the study period, pairs of adult

females that were tracked simultaneously only spent 45-80% of their time together, yet their home-ranges overlap extensively between individuals and between years. On average, buffalos stay together about 3.7 days (sd=1.0 day) before splitting and reunite after about 2.3 days (sd=0.7 day) spent apart.

Total seasonal occupancy was modelled by summing the individual Utilization Distributions (UD) using the biased random bridges for movement-based kernel density estimation approach (Benhamou 2011; Cornélis *et al.* 2011). Fine scale buffalo habitat selection was modelled with Step Selection Functions (SSF). Movement paths of buffalo were decomposed into a series of steps (i.e. straight-line segments linking successive 1 h locations), and each step was paired with 10 random steps to create a stratum. Random steps had the same starting location as observed steps, but differed in that length and turning angle were randomly drawn from the empirical distribution of step lengths and turning angles obtained by pooling steps data from all other individuals, as recommended by Fortin *et al.* (2005) and Forester *et al.* (2009). Control steps were obtained using the 'hab' R package (Basille 2015). We estimated SSF parameters using conditional logistic regression within a generalized estimating equation (GEE) framework.

Temporal autocorrelation between the steps can bias the standard errors of parameter estimates. Following Forester *et al.* (2009), we determined the autocorrelation time lag was of 3 hours for buffalo. As ruminants, buffalo alternate 3-5h active foraging bouts with resting and rumination (Sinclair 1977). Natural breakpoints between these bouts emerged at 4h, before the morning bout, 12h, before the evening bout and 20h, before the night bout (Figure 42a). We chose to run three separate SSF models on each one of the 3 daily foraging periods. We calculated robust standard errors after having grouped all steps occurring the same foraging bouts in independent clusters (Fortin *et al.* 2005; Craiu, Duchesne & Fortin 2008). Since bouts belonging to each foraging period were analyzed in separate models, clusters separated by at least 16h, thus guaranteeing statistical independence. We considered each bout statistically independent, but if different collared individuals were within 300m of one another during a given bout, their locations were attributed to a single cluster. Steps shorter than 30m were discarded since they correspond to resting or ruminating behavior. Since buffalo herds are constantly mixing or splitting, it appeared futile to try and distinguish herd effects from individual effects with such a small sample size.

SSF independent variables included one categorical variable: *vegetation type*, a linear and a quadratic term for *distance to the boundary* (bound) and *distance to water* (water). Distance to water was calculated on a daily basis as pans dried up during the 2013 and 2014 dry seasons. The model included relative *cattle density* obtained from the IPP model as well as the interaction between *distance to the boundary* and *distance to water* and *vegetation type,* respectively.

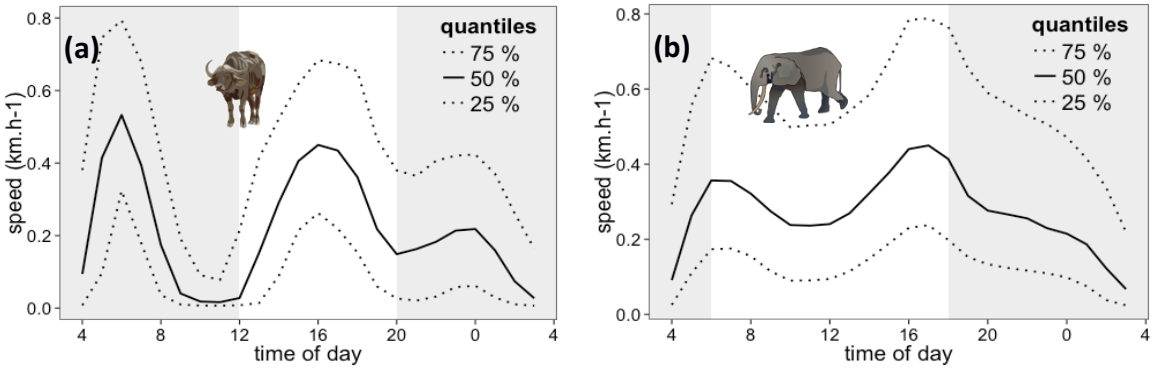


Figure 42: Hourly speed according to time of day: (a) Buffalo alternate three foraging and resting bouts whereas (b) elephant bulls have two more diffuse activity peaks at dawn and dusk

2.4 Modelling elephant habitat selection

Initially, 6 bulls were captured in Sikumi Forest and collared in December 2010. One was shot as a problem animal in February 2011 and another in a trophy hunt in March of the same year. The data from these two individuals was discarded since they did not cover all three seasons. However, both collars were retrieved and fitted on other bulls in April 2011. All collars provided hourly GPS locations until February 2013 with the exception of one of the refitted collars that ended in November 2012 (Chloé Guerbois pers. Comm.).

Statistical methods were similar to the ones conducted for buffalo at the two spatial scales. Unfortunately, distance to water was estimated for each season because no monitoring of pan dry up had been conducted in 2010 and 2011. In spite of considerable range overlap, elephant bulls range independently and spend less than 1% of their time together. Unlike buffalo that moved as a cohesive herd, individual variability was accounted for by using a mixed conditional logistic regression model (Duchesne, Fortin & Courbin 2010) using the TwoStepCLogit package version 1.2.3 in R (Craiu *et al.* 2011). The first step consists in the evaluation of model parameters for each cluster (in our case individual) independently. The second step estimates population level parameters and the matching random effects for each individual's parameters (Craiu *et al.* 2011).

Being monogastric herbivores, elephants do not have the clear-cut succession of active foraging bouts and resting and ruminating (Figure 42b). Since cattle enter the Forest area during the daytime and elephant excursions into Communal land generally occur at night, daytime and nighttime habitat selection patterns were estimated separately for each season.

3 Results

3.1 Seasonal changes, herding practices and surface water availability determine cattle use of the forest area.

Data obtained from GPS collars confirm patterns described by cattle owners and herd boys. Cattle incursions in Sikumi Forest differ markedly between seasons. During the rainy season cattle are driven into the Forestry area nearly every single day (median=95% of days, Table 4) they range about 1.6km (Table 5) from the boundary but may reach up to 5.4km and spend on average 4.3h inside (Table 6). During the cold dry season, cattle seldom enter the forestry area (median = 17% of days), incursions are briefer (mean=1.8h) and closer to the boundary (mean=0.8km, max=3.8km). As for the hot dry season, cattle enter the Forestry area more often (median=31% of days), stay longer (mean=3.1h) and travel further (mean=1.4 km, max=6.0 km).

Table 4 : Number of days cattle entered Sikumi (given as a percentage of the total number of days) from a given season spent inside Sikumi for each collared cattle.

Id	rain	Cold dry	Hot dry	Id	rain	Cold dry	Hot dry
Di7	98%	13%	29%	**Mb9**	38%	5%	26%
Jw3	99%	26%	34%	**Mg6**	68%	68%	-
Jw4	70%	17%	10%	**Mg8**	95%	30%	51%
Lu9	84%	13%	6%	**Si5**	96%	24%	58%
Mb2	98%	7%	3%	**Si6**	99%	26%	54%
Mb8	87%	9%	33%				

Table 5 Maximum distance to the boundary by season (km)

Id	Rain (mean ± sd)	Colddry (mean ± sd)	Hot dry (mean ± sd)
Di7	1.4 ±0.8	0.5 ±0.8	1.0 ±1.1
Jw3	2.2 ±0.5	0.6 ±0.5	1.8 ±1.6
Jw4	1.1 ±0.7	0.8 ±0.5	1.4 ±1.3
Lu9	0.9 ±0.6	1.0 ±0.4	0.7 ±0.3
Mb2	1.6 ±0.5	1.7 ±0.5	1.0 ±1
Mb8	1.6 ±0.6	1.2 ±0.9	1.1 ±1.2
Mb9	1.4 ±0.8	0.7 ±0.6	1.4 ±1.3
Mg6	1.1 ±0.4	0.4 ±0.4	- -
Mg8	0.8 ±0.6	0.2 ±0.3	0.5 ±0.7
Si5	2.3 ±0.8	1.6 ±1.3	1.8 ±1.3
Si6	2.2 ±1	1.2 ±1.2	2.0 ±1.3

Table 6 Average time spent in the Forest Area by day (hours)

Id	Rain (mean ± sd)	Cold dry (mean ± sd)	Hot dry (mean ± sd)
Di7	3.8 ±1.4	1.3 ±1.7	2.6 ±1.8
Jw3	4.7 ±1.2	0.2 ±0.6	3.2 ±2.3
Jw4	1.8 ±1.3	0.4 ±0.6	2.2 ±2
Lu9	3.3 ±1.7	2.9 ±1.1	1.9 ±1.1
Mb2	4.4 ±1.3	3.8 ±1.5	1.7 ±1.7
Mb8	4.1 ±1.4	2.0 ±1.5	2.4 ±2.2
Mb9	3.9 ±1.6	1.9 ±1.7	4 ±2.7
Mg6	5.4 ±2.2	2.1 ±2.7	- -
Mg8	6.0 ±2.3	1.9 ±3	2.5 ±3.1
Si5	5.0 ±1.1	2.6 ±2	3.9 ±2.5
Si6	5.2 ±1	1.8 ±2	3.3 ±1.8

Overall cattle habitat selection patterns reflect the strong central place effect of their home kraal shown by the strong decrease in probability of selection as distance to the boundary increases regardless of distance to water and habitat type (Figure 43). Interestingly, the model managed to capture the trade-off between a strong negative effect of the distance to the kraal and the weak positive effect of the distance to the boundary suggesting cattle might range further inside the protected area if they were not forced to return to the Communal Area every night. Cattle strongly select for areas close to water pans during the rainy season. The pattern dampens in the cold dry season as the pans dry up and is actually reversed in the hot dry season (Figure 43). Unsurprisingly, cattle systematically select for the most open habitats, especially near water pans and use areas close to the boundary more intensively. However, as the dry season advances, the difference between habitats decreases. As a result of their movement patterns, cattle presence is much less predictable yet their distribution follows a monotonous gradient away from the boundary regardless of vegetation types or distance to water pans.

3.2 Consistent spatial avoidance of cattle by buffalo

The resident buffalo herds utilize their entire home-range throughout the year. The study area only encompasses a portion of their home-range: They spend 62% of their time in the study area during the rainy season, 77% during the cold dry season and 47% during the hot dry season. Overall, buffalo range between 500m and 15km of the boundary of Sikumi Forest. They strongly avoid areas used by cattle and they intensify or reduce their use of the boundary area according to seasonal variations in cattle presence (Figure 44, Table 7).

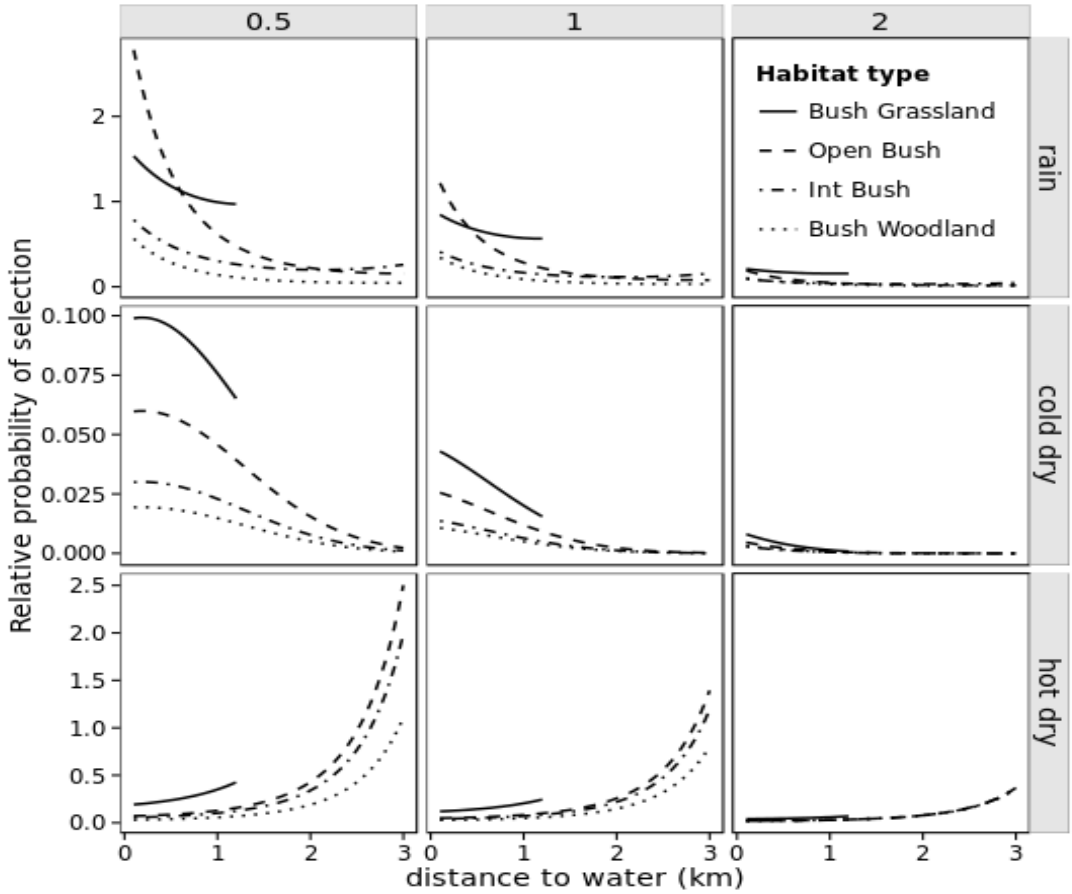


Figure 43: Cattle probability of selection in different habitats according to distance to water, distance to boundary (500m , 1km and 2km) and season (rain, cold dry and hot dry).

During the rainy and cold dry seasons buffalo spend only 2.5% and 1.9 % of their time within the areas used by cattle whereas the proportion of time spent within 3km of the boundary doubles from 7% to 13%. As cattle reduce their range inside the forest area during the cold dry season, buffalo substantially increase their use of areas close to the boundary (Figure 44c). As water availability decreases during the hot dry season, buffalo contract their home-range around the remaining natural and especially pumped water pans. As a result, they spend most of their time beyond the range of cattle incursions (Figure 44c). As cattle range further inside the forest, substantial overlaps (Table 7) appear around permanent waterholes or corridors between them. However, these overlaps do not necessarily imply increased contact rates. Collared buffalo and cattle followed in synchrony were within less than 1km of each other on only two occasions during the entire 2010 and 2013 hot dry seasons, along the corridor between 2 major pans just north of the Hwange National Park airport (Figure 44c). Beyond large scale seasonal patterns, buffalo fine scale avoidance of cattle varies according to seasonal changes in cattle occurrence, surface water distribution, as well as buffalo foraging strategy and drinking requirements. Buffalo habitat selection patterns are more consistent within each bout than between bouts, as described hereafter (Figure 45Figure 46).

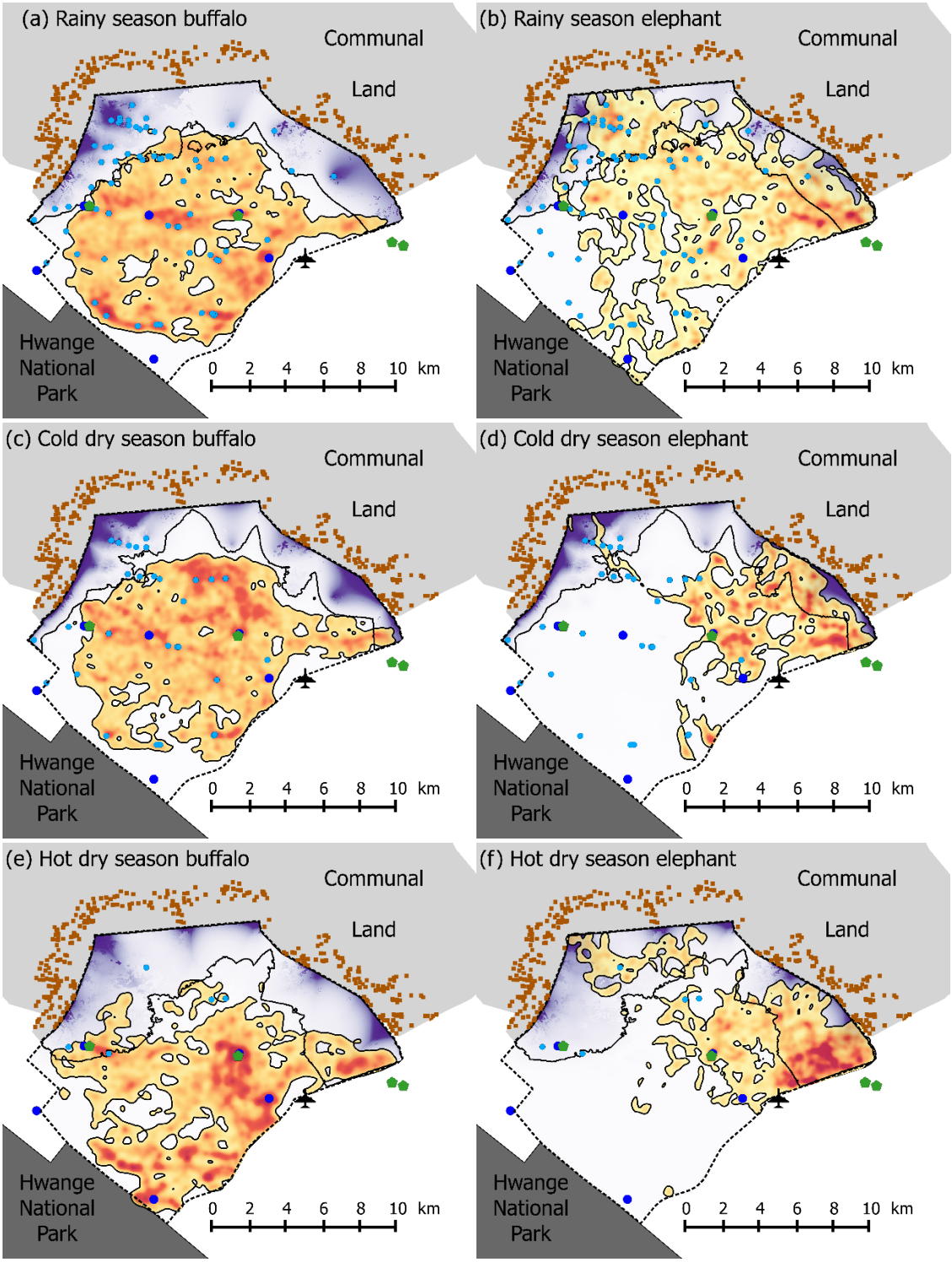


Figure 44 Seasonal range overlap between buffalo (left) or elephant (right) utilization distribution (orange) and cattle predicted distribution (purple) by season (top: rainy season, middle: cold dry season and bottom: hot dry season) within the Sikumi Forest Area. Darker orange (resp purple) areas are more intensively used. The 321 kraals used to predict cattle locations are show as brown squares. Remaining natural pans are shown in sky blue and artificial water pans in dark blue. Safari Lodges located close to the boundary, which provide water to wildlife, are represented as green pentagons.

Table 7: Percentage overlap of buffalo and elephant utilization distribution volume with cattle predicted utilization distribution volume.

season	% Elephant Bull HR in cattle HR (n=6)	% Buffalo HR in cattle HR (n=1)	% Cattle HR in elephant Bull HR (n=6)	% Cattle HR in Buffalo HR (n=1)
rain	21-67	2.5	35-59	3.0
colddry	15-42	1.9	4-23	1.1
hotdry	18-66	10.6	7-44	12.3

3.2.1 Buffalo habitat selection during the morning bout

During their morning foraging bout, (from 4h to 12h) buffalo seek out open areas far away from water during the rainy season. The limited overlap between cattle and buffalo is explained by consistent selection of areas away from the boundary and an even stronger avoidance of areas used cattle. The selection for areas further from waterholes and open habitats dampens as distance to the boundary increases (Figure 45). Buffalo continue staying away from the boundary during the dry season, but no longer avoid areas specifically used by cattle. Buffalo selection shifts closer to water during the dry season to the point they prefer areas close to water during the hot dry season. Over the same time period buffalo habitat selection intensifies during the cold dry season as they select open areas and avoid wooded areas. Selection for open areas subsequently disappears during the hot dry season when distance to water and the boundary become the sole movement criteria (Figure 45).

3.2.2 Buffalo habitat selection during the evening bout

Buffalo prefer to drink on a daily basis and their favorite drinking time is dusk. Accordingly, buffalo seek out the closest water pan during the evening bout (from 12h to 20h) (Figure 46). During the rainy season they stay away from cattle and the boundary, however during the cold dry season they still avoid cattle but no longer stay away from the boundary and during the hot dry season neither the distance to the boundary nor cattle presence determine their movement decisions (Figure 46). Surprisingly, we found no effect of distance to water during the evening bout in the hot dry season. However, during the hot dry season, buffalo have already selected for areas close to water during the morning foraging bout. Since they do select for open habitats that only occur within 1km of water they probably remain close to water until sundown.

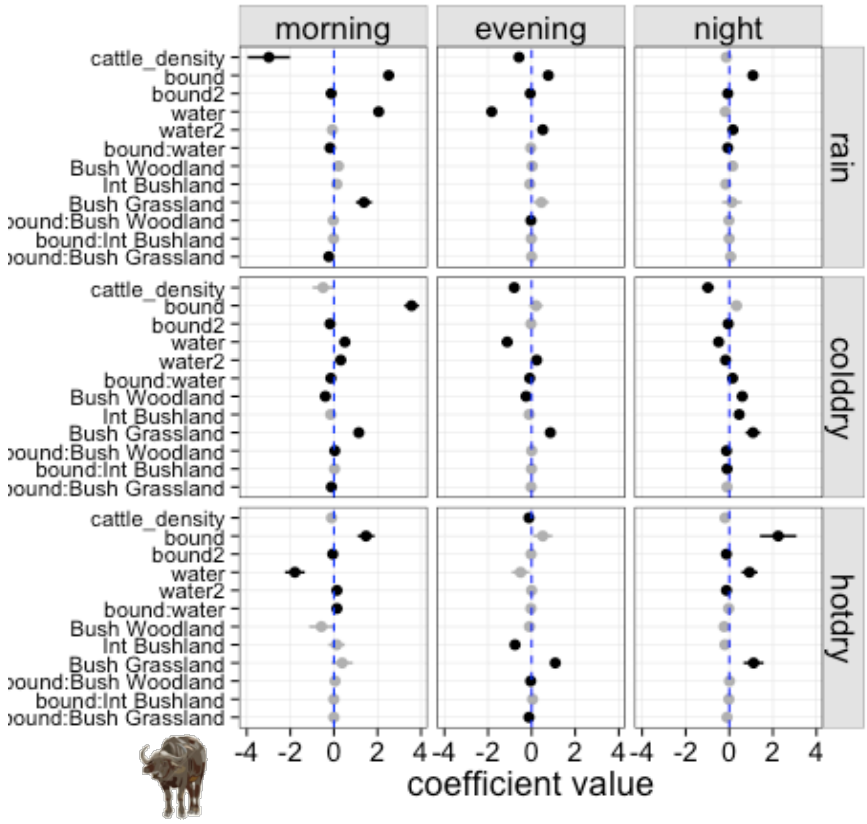


Figure 45: Buffalo SSF parameters (± standard error) by foraging bout and season. Each bout includes a peak in foraging activity: morning (4h-12h), evening (12h-20h) and night (20h-4h) (Figure 42a). Significant parameters are shown in black non-significant ones in grey. The effects of the categorical variable vegetation and the vegetation x boundary interaction are relative to "Open Bushlands" that served as a reference factor level.

3.2.3 Buffalo habitat selection during the night-time bout

Buffalo are much less mobile during the night (from 20h to 4h) than during day (Figure 42). Yet buffalo do not avoid the boundary as strongly than during daylight hours and we only found a weak avoidance of areas used by cattle during the cold dry season (Figure 45). However, this pattern of avoidance results from buffalo ranging close to the boundary at night during the cold dry season as shown by the negative quadratic effect. Surprisingly, we report no habitat preference at night during the rainy season; unlike the cold and hot dry season when buffalo actively seek out open areas close to water. Buffalo take the opportunity to range away from water during the cooler nighttime hours of the hot dry season.

Despite apparently similar selection for open habitats, buffalo reduce the likelihood of encountering cattle all year around by staying away from the boundary and avoiding areas intensively used by cattle whenever they get closer to the boundary. In addition, buffalo stay away from waterholes during the day and come to drink at dusk after cattle have left during the rainy season and the cold dry season. Interestingly, buffalo select areas close to water during their morning bout in the hot dry season at a time of the year when cattle no longer select these areas.

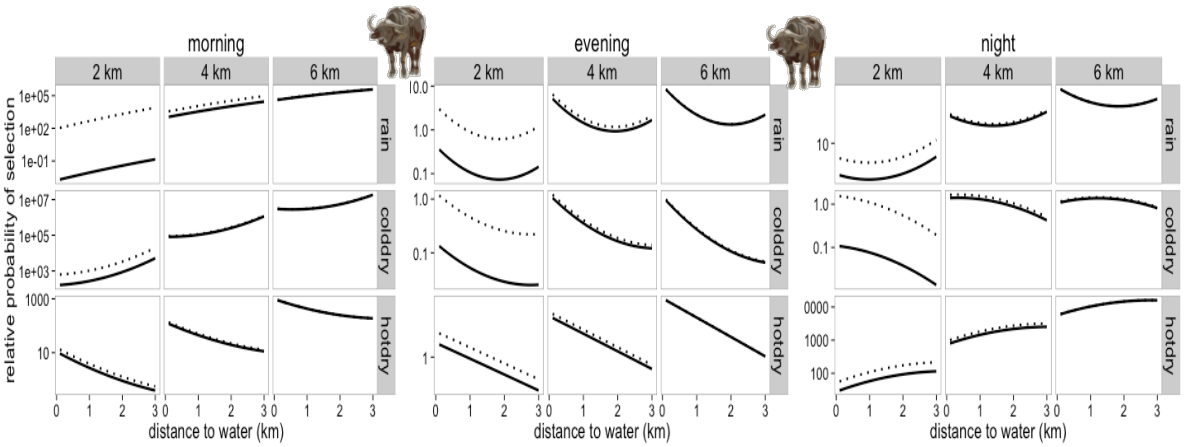


Figure 46: Buffalo relative probability of selection predicted by the SSF during each foraging bout according to distance to water, season and distance to boundary. Model predictions including cattle density are shown by full lines. Dashed lines predict potential relative probability of selection in the absence of cattle. Note the log-scale on the y axis.

3.3 Elephant's large scale overlap but small scale avoidance.

The study area only includes about one third of each elephant bull's home-range that cover on average 420 km^2 (sd=60). Unlike buffalo, elephant bulls extensively use the area occupied by cattle which covers 15% to 68% of each individual's seasonal home-range; with considerable variation between individuals and seasons (Table 7 & Figure 44). Over the study period, the 6 elephant bulls spent a total of 1960 nights in the study area (between 226 and 334 nights per individual) yet they only entered the communal land on 79 occasions, given the sampling frequency of GPS locations (4-24 excursions per individual). Excursions nearly exclusively occurred at night throughout the year with two peaks: half of the excursions occur within 3 months during the hot dry season whereas 25% of excursions occur at the end of the cropping season between March and May.

In spite of this apparent overlap, elephant bulls generally avoid the forest boundary and areas with high cattle density (Figure 47). However, the pattern is nonlinear: The linear *distance to boundary* term reveals elephant bulls avoid the boundary less strongly during the day than during the night. The quadratic *distance to boundary* term reveals that in the daytime elephants select for areas between 4km and 6km from the boundary in the rainy season, only 3-4 km from the boundary during the cold dry season and 4-5km from the boundary during the hot dry season (Figure 48). At night, during the rainy and cold dry seasons, elephant bulls weakly avoid the boundary but strongly avoid areas that were used by cattle during the day during the same season. Conversely, they select for areas closer to the boundary in the hot dry season (3-4km) and take advantage of the night to forage in areas cattle use in the daytime.

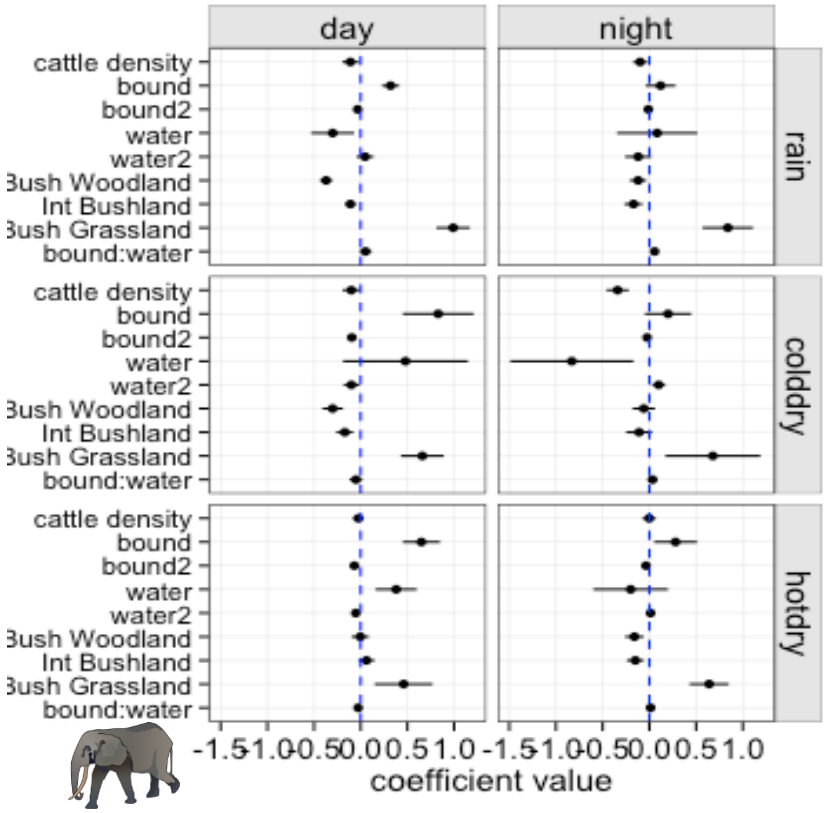


Figure 47: Elephant SSF parameters (± standard error) for day and night bouts by season The effect of the categorical variable vegetation is relative to "Open Bushlands" that served as a reference factor level. Linear and quadratic effects were included for distance to water (water,water2) and distance to the boundary(bound, bound2).

Elephant bulls unexpectedly select for open areas throughout the year. However the intensity of selection decreases during the dry season (Figure 48). Like cattle, elephant bulls also prefer staying close to water during the rainy season but shift their selection 1-2 km away from water during the cold dry season and more than 3km away during the hot dry season. The pattern is reversed in the nighttime, when elephants prefer areas 1-2 km away from water in the rainy season, have no preference for any particular distance during the cold dry season, and strongly select for areas close to water during the hot dry season (Figure 48). Elephant habitat selection suggests a strong potential overlap with cattle as both species shift their preference away from water as the dry season advances. In practice, elephant bulls avoid areas used by cattle during the daytime.

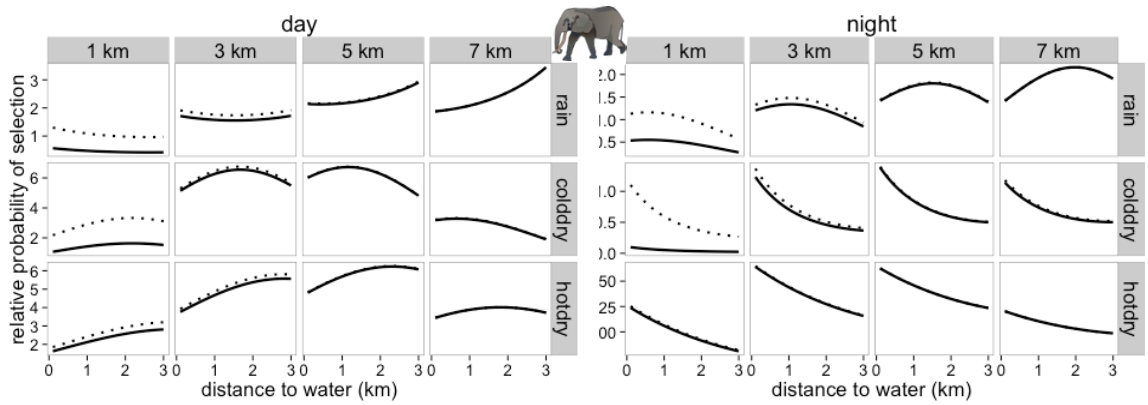


Figure 48: Elephant relative probability of selection predicted by the SSF during the day and during the night according to distance to water, season and distance to boundary. Model predictions including cattle density are shown by full lines. Dashed lines predict potential relative probability of selection in the absence of cattle.

4 Discussion

Surface water availability is the key determinant of large herbivore distribution in semi-arid and arid ecosystems. All three species considered in this paper are water dependent and prefer open grassland habitats that are associated with water pans in the bushland and woodland savannas that dominate Sikumi Forest (Figure 43Figure 45 Figure 47). However, neither domestic nor wild herbivores are free to use these habitats according to their preference. Cattle incursions are strongly constrained by the central place effect of their home kraal that keeps them from wandering beyond a few kilometers from the boundary (also see Butt 2011). Wildlife movement is also constrained by the boundary of the protected area. With the exception of few crop and garden raiding events by elephant bulls, wild herbivores remain well within Sikumi Forest. Moreover, both species actively avoid areas used by cattle. These patterns are consistent with displacement of grazing herbivores and elephant by cattle reported in the W transfrontier park (Hibert *et al.* 2010) and general avoidance of cattle by wild herbivores (De Leeuw *et al.* 2001; Stewart *et al.* 2002; Ogutu *et al.* 2014).

4.1 The effects of seasonality on cattle-wildlife distribution and avoidance patterns

Seasonal changes in habitat selection at both large and fine scales shed light on the roles of surface water availability and forage abundance on the interaction between wildlife and cattle/people at the edge of a protected area. As the dry season advances, cattle distribution becomes less predictable as they shift away from open areas close to water in their search for forage. They range further away from the dried up pans and deeper into the protected area suggesting that during the dry season intraspecific competition may be a stronger driver of cattle habitat selection than competition with wildlife (Young, Palmer & Gadd 2005; Odadi *et al.* 2011) or the risk of encountering predators (Kuiper *et al.* 2015).

Buffalo and elephant also shift their distribution albeit at different spatiotemporal scales. Buffalo avoid cattle at large scales with minimal home-range overlap yet they will readily shift their home-range closer to the boundary in order to exploit areas freed by cattle during the cold dry season. Such flexible movement patterns are facilitated by widespread surface water availability during the cold dry season which allows buffalo to exploit these areas without coming into contact with cattle (Figure 44). Buffalo strategy changes in response to cattle behavior and water availability. During the rainy season, the negative effect of cattle density on buffalo habitat selection was strongest during the morning bout when cattle and negligible at night when cattle were absent. As the dry season advances, buffalo stay away from the boundary but no longer specifically avoid cattle during their morning bout, a behavior consistent with the unpredictable distribution of cattle during the dry season. In the evening, buffalo shift to fine scale habitat selection, they no longer avoid the boundary but avoid water pans where cattle were present during the day. By the end of the dry season, buffalo and cattle home-range overlap increase fivefold and buffalo no longer avoid areas of high cattle density thus explaining the relatively higher likelihood of contacts between both species and the greater risk of disease transmission (Miguel *et al.* 2013). Indeed, buffalo strongly contract their home-range around waterholes during the dry season (Ryan *et al.* 2006; Cornélis *et al.* 2011) and only venture further away from water during their nighttime foraging bout. Buffalo being bulk feeders, it is unlikely they can afford to avoid cattle in times of forage scarcity such as the peak of the dry season. Spatial overlaps between buffalo and cattle reflect the distribution of water pans pumped by safari operators. Overlap was greatest along a corridor joining two major water pans in the east of the study area (from 1km to 6km from the boundary) and around one pan in the west located 2km from the boundary. Considering cattle drink at boreholes within the communal land and buffalo remain in close proximity to water, potential contacts and disease transmission may be reduced by shifting artificial waterholes further away from unfenced protected area boundaries. Such policies might also reduce livestock depredation (Kuiper *et al.* 2015) as predators will select for areas with higher wild prey densities and remain close to permanent waterholes (Valeix *et al.* 2010).

Unlike buffalo, elephant bull home-ranges largely overlap with cattle, yet elephant bulls stay away from the boundary, water pans and particularly areas used by cattle during the day but move back closer to the boundary and to water at night when cattle are gone (Figure 48). The difference between elephant bulls and buffalo may reflect the effects of strong exploitation competition between cattle and buffalo that effectively excludes buffalo from areas used by cattle as opposed to the effects interference competition on elephant bulls during the day, but not at night while cattle are kept in their kraal. Moreover, as the dry season advances, elephant bulls select for areas closer and closer to the boundary during the night. Finally, the unexpected nighttime selection by elephant bulls of areas used by cattle during the hot dry season further suggests that for elephant bulls as well, intraspecific competition is a stronger driver of habitat selection as elephant bulls gradually focus on areas that harbor the lowest densities of both male and female elephant when forage becomes most limiting. Elephant

bulls using these areas might have a subordinate status and have been excluded from safer foraging areas further inside Sikumi Forest and Hwange National park by dominant individuals (Paper *et al.* 2007).

4.2 Avoidance of cattle or avoidance of people?

Whereas cattle and buffalo hardly overlap and almost never meet in Sikumi, up to 60% of elephant bull's seasonal home-range can be found within the area utilized by cattle. Similarly, elk have been reported to mingle with cattle whereas mule deer do not (Dohna *et al.* 2014). More generally livestock may effectively displace other herbivore species completely (Stewart *et al.* 2002; Kittur, Sathyakumar & Rawat 2010; Hibert *et al.* 2010), they may overlap in space but not in time (Cooper *et al.* 2008; Atickem & Loe 2014) or even co-mingle (Dohna *et al.* 2014). Such differences may even occur for the same species at different study sites. For instance, buffalo strongly avoid cattle in Sikumi Forest whereas their range overlap much more extensively with cattle around the Greater Limpopo Transfrontier Conservation Area (Miguel *et al.* 2013). Thus, the mere presence of cattle is insufficient to explain their propensity to effectively deter wildlife.

Behavioral cues may repel animals when associated with a perceived risk such as encountering predators or people (Jachowski, Slotow & Millspaugh 2014). For elephant these can consist in disagreeable encounters with chili peppers (Parker & Osborn 2006) or bees (King, Douglas-Hamilton & Vollrath 2011), however people remain the best deterrent (Hedges & Gunaryadi 2010; Guerbois, Chapanda & Fritz 2012). Rather than avoiding cattle per se, buffalo and elephants might in fact be avoiding humans. During the rainy season, herd boys drive cattle into Sikumi Forest and remain with them for the entire day. However, cattle often enter unaccompanied during the dry season. Unfortunately, cattle movement patterns reflect herding practices, one cannot tell whether elephant and buffalo's usage of areas closer to the boundary result from the absence of herd boys or from smaller and less frequent cattle incursions. As the dry season progresses and forage becomes scarcer, cattle are less likely to spontaneously return to the communal area and herd boys are sent to fetch them in the late afternoon. Even though cattle are not systematically accompanied by people, the association may be sufficiently strong for wildlife to consider the sound of cow bells and the smell of cattle as a cue for human presence.

However, various studies reported the displacement of wild herbivores by free ranging cattle that are not associated with human presence (Stewart *et al.* 2002; Cooper *et al.* 2008). Nor does the presence of cattle herders necessarily imply a greater displacement of wild herbivores. In East-African savannas, sedentarisation of nomadic pastoral communities resulted in a decline in herbivore abundance attributed to displacement from key grazing resources by resident livestock (Western, Groom & Worden 2009). The decline neither resulted from increased offtake nor from higher cattle densities: A neighboring nomadic community with similar human and livestock population growth witnessed an increase in

wildlife abundance over the same period. Moreover, in southern Kenya, Masai pastoralists preferentially take their cattle to forage far from water during dry periods and commute large distances between their pastures and water. Such practices ease coexistence with wild herbivores species that select foraging grounds along the distance to water gradient according to their water dependency (Sitters *et al.* 2009). Herding practices in Sikumi Forest consist in repeated incursions by sedentary livestock to the same areas close to water. Unlike patterns reported by Sitters *et al.* (2009) and as suggested by Western *et al.* (2009) herding practices in Sikumi Forest may effectively exclude wild herbivores from the vicinity of the Forest boundary.

4.3 Edge effects at an unfenced interface

Despite the absence of any physical barrier to movement, buffalo never cross into the communal land and elephant bulls make rare excursions during the rainy and hot dry seasons. Moreover, both species underutilize the boundary area as reported for real fences in Kruger NP (Vanak, Thaker & Slotow 2010). During the cold dry season buffalo utilization density is higher close to the boundary of their home-range than further inside the protected area. Throughout the year, elephant bulls select for intermediate distances to the boundary. As a result, both species avoid Sikumi Forest boundary but bunch up against a virtual fence (Jachowski, Slotow & Millspaugh 2014)corresponding to the contour of the area used by cattle. Elephants have been reported, to bunch up against fences surrounding Etosha National Park (Loarie, van Aarde & Pimm 2009). The boundary of Sikumi Forest has substantial edge effects on wildlife that are comparable to effects of real barriers. The patterns described are similar to caribou aggregation close to anthropogenic features described by Fortin *et al.* (2013). However, in Sikumi Forest, we identified cattle incursions and the distribution of surface water as the template for these patterns that may be expected around other protected areas. Displacement of wildlife on the boundary of protected areas might promote coexistence for large conservation areas such as the Kavango-Zambezi TFCA that encompasses both Hwange National Park and Sikumi Forest. However these edge effects may be substantial for smaller conservation areas.

4.4 The importance of surface water in an increasingly arid landscape

Drought severity in Sikumi Forest and surrounding areas has worsened over the course of the 20th century (Chamaillé-Jammes, Fritz & Murindagomo 2007a). These patterns are similar to those reported in South Africa (van Wilgen *et al.* 2015). In Southern Africa, rainfall is expected to decrease and and temperatures to rise during the 21st century (Giannini *et al.* 2008). Reductions in rainfall have two effects: A decrease in primary productivity and thus dry season forage quantity and a reduction in available habitat earlier on during the dry season as natural pans dry up. However, artificial water provisioning substantially buffers the reduction of available habitat (Chamaillé-Jammes, Fritz & Murindagomo 2007b) which may be marginal in Sikumi Forest due to the high density of artificial water pans. Unfortunately, GPS monitoring

was concomitant with years of average rainfall, neither buffalo nor cattle were collared during the 2011 - 2012 drought. During a drought, forage scarcity and crop failure would induce cattle to range even further inside the protected area (Butt 2014). In Sikumi Forest, the 1992 drought was a turning point when traditional authorities and the Forestry Commission came to an informal agreement to tolerate cattle incursions within the first few kilometers to mitigate a massive die off in domestic livestock. In addition, wildlife would aggregate in larger numbers around the remaining water pans (Valeix 2011), leading to higher risks of disease transmission (Miguel *et al.* 2013). Thus, during a drought, one might expect hot dry season conditions to prevail earlier on during the dry season and persist longer in the case of delayed rains. These conditions are mainly characterized by greater cattle incursions and reduced buffalo mobility leading to a higher overlap between cattle and buffalo as well as selection for areas closer to the boundary by elephant.

5 Conclusion

Cattle are ubiquitous and highly valued in most agro-pastoral societies that live around protected areas worldwide. However, cattle incursions into protected areas are often perceived as “unnatural” and considered as a threat to wildlife via overgrazing (Butt 2014). The potential for cattle owners and their herds to displace, yet avoid, species such as buffalo and elephant may in fact provide the baseline for coexistence. In order to maintain the integrity of protected area boundaries, two mechanisms may be mobilized: fear of humans and resource availability. In arid lands, water provisioning may be designed to allow for the segregation of livestock and wildlife in order to avoid conflict. However, in more mesic landscapes, such as savannas during the rainy season, the relation between cattle and wildlife may be one of facilitation rather than competition (Voeten & Prins 1999; Odadi *et al.* 2011). Nonetheless, cattle may only be perceived as cues for human presence, thus traditional herding practices, which often relies on people accompanying cattle, may be paramount to maintaining segregation between cattle and wildlife.

General Discussion

Figure 49: Heading to water. Elephant family group approaching a waterhole.

Like many arid rangelands, the Hwange ecosystem has been profoundly modified by human activities over the past two centuries. The 19th century was characterized by the demise and near extirpation of large herbivores due to hunting and ended with the rinderpest epidemic that swept through Africa (Vandewalle & Alexander 2014). The 20th century saw the recovery of wildlife populations and particularly elephants which became the dominant herbivore in Hwange National Park (Fritz et al. 2011). Artificial water provisioning was the most important factor involved in this recovery. The Hwange elephant population started to increase after the first boreholes were sunk and seasonal pans were transformed into perennial water sources (Davison 1967). Over the course of decades, the network of artificial waterholes spread and herbivore populations grew. The present day population, of about 40 000 elephants inhabiting Hwange, largely depends on the areas where artificial water sources are maintained to survive throughout the dry season. Thus, patterns and processes described in this thesis occur in a novel ecosystem with no historical precedent (Hobbs, Higgs & Harris 2009) where key processes such as surface water distribution are directly under human control. However, Hwange shares this trajectory with many African savanna ecosystems for which management decisions such as fencing, water provisioning or culling have determined the fate of animal populations (Cumming 1981; Walker et al. 1987; Hayward & Kerley 2009). The constraints of

surface water availability can be found throughout the world in arid rangelands that have been transformed by water provisioning (James et al. 1999). Within this context, the movement pattern of elephant, the dominant herbivore in our study system, sheds light on the key role played by surface water on their migratory behavior (chapter 1), foraging behavior (chapter 2) and habitat selection (chapter 3). We will review each one of these roles in turn before synthesizing the results within the perspective of the aridification under way due to climate change and conservation outside of protected areas (chapter 4).

1 Water and the timing of a partial migration

The partial elephant migration in Hwange is most likely the largest and longest extant elephant migration in Southern Africa. As soon as cumulated rainfall is sufficient to start filling up seasonal water pans, migrants travel west or south west over a period lasting from several days to several weeks. After a single rainfall event swept through the center of the park on October 22nd 2013, migrant elephants moved out to the area (pers. obs.), however the absence of rainfall during the following month forced them back to their dry season home-ranges (pers. obs.). The timing and progression of the return trip were unique to each collared individual, yet largely consistent between years. Two trends emerged: (i) elephants return to their dry season home-range later in years with better rainfall, presumably as long as surface water persists in their rainy season range, (ii) elephants shift their dry season home-range west in years with higher rainfall where waterhole density is lower. These patterns will need to be confirmed by studies during years with more contrasted rainfall.

Migrant elephant family groups travel 30% to 100% more than resident family groups during the rainy season and 20%-50% more during the dry season (Figure 50) suggesting migration may come at a considerable cost. The advantages of migrating for elephants in Hwange remain to be explored. Similar differences in movement patterns between migratory and resident individuals have been described for elephants in Samburu, Kenya, and have been linked to social status (Wittemyer *et al.* 2008; Polansky, Douglas-Hamilton & Wittemyer 2013). Density dependence effects could be one of the drivers of partial migration in Hwange with resident source populations and migratory sink populations. Alternatively, migratory elephants may have access to better rainy season foraging resources (Chapman et al. 2011; Gaidet & Lecomte 2013). Large herbivore migrations in tropical systems often occur along fertility and/or rainfall gradients (Holdo, Holt & Fryxell 2009; Naidoo *et al.* 2012; Bartlam-Brooks *et al.* 2013; Bohrer *et al.* 2014). Hwange NP is characterized by a north-east to south-west rainfall gradient. Migratory elephants may thus travel down the rainfall gradient to areas exhibiting greater forage quality that would counterbalance the energetic cost of migration. Further studies will need to assess the proportion of migrants, resource quality during the rainy season and the age structure of migratory family groups to assess potential fitness differences between the two life history strategies. Our preliminary results suggest the heterogeneity of rainfall patterns and waterhole dry up are major drivers of migratory patterns. The benefits of migrating may therefore depend on inter-annual variability in surface water availability.

Future studies should also bear in mind this migration pattern is fairly recent and strongly associated with dry season water distribution in Hwange National Park. The migration may be a truncated remnant of historical migrations to the perennial Gwayi River and its tributaries only a few dozen kilometers to the East (Davison 1967), calling for the integration of these patterns in the development of the Kavango-Zambezi Transfrontier Conservation Area. However, part of the population increase following the end of culling operations has been attributed to immigration (Chamaillé-Jammes et al. 2008). Thus, long distance migrants might be returning to their former ranges. It is unknown whether migrants and residents belong to the same or to different populations.

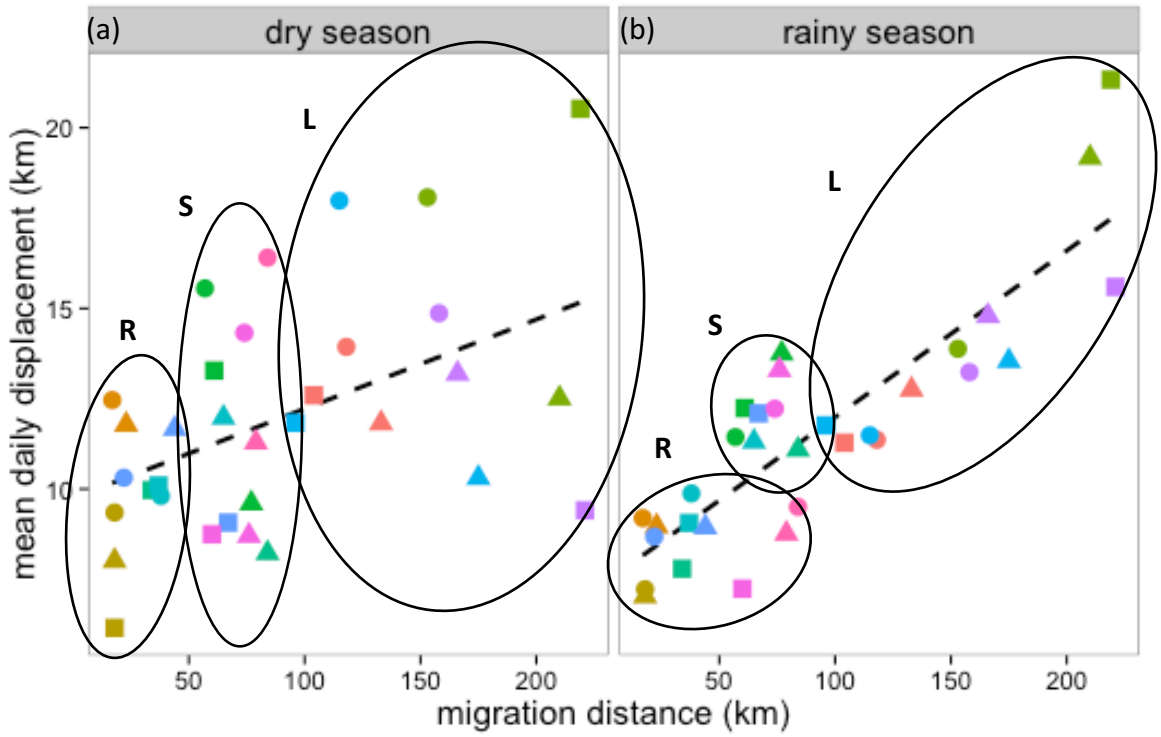


Figure 50: Migrants cover longer daily distances than residents. Daily displacement (DD) is the total distance covered in 24h, migration distance was defined as the distance between the dry season home-range centroid and the furthest point from the centroid during the rainy season. DD was calculated during the stationary phase during (a) the dry season and (b) the rainy season. (a) Mean DD was weakly correlated with migration distance during the dry season (R2=0.19, slope=2%) and (b) strongly correlated with migration distance during the rainy season (R2=0.74, slope=4%) in 2012-2013 (circle), 2013-2014 (triangle) and 2014-2015 (square). Each individual is represented by a different color, ellipses show residents (R), short distance migrants (S) and long distance migrants (L). Note the transition phases (i.e. migration events) were not included in daily displacement calculations.

2 Central place effects of water in semi-arid savannas

Our study revealed that elephants mitigate the trade-off between drinking and foraging constraints during the dry season by (i) making directed movement between waterholes and their feeding grounds, (ii) increasing travelling speed and (iii) shifting towards briefer trips. These results leads us to discuss the importance of allowing movement parameters such as speed and sinuosity to vary in foraging models and to consider how the inclusion of the central place resource (i.e. water) might alter the currency in central place foraging models.

2.1 The determinants of optimal travelling speed in a terrestrial herbivore

Current central place foraging models explicitly consider constant travelling speed and variable trip durations (e.g. Olsson, Brown & Helf 2008; Olsson & Bolin 2014). Such assumptions may be valid for predators searching for their prey when the central place is a nest or a burrow. However, for many animals there might be stronger constraints on keeping constant trip duration than constant travelling speed. Trip duration can result from central place resource requirements such as drinking water for large herbivores (Cain, Owen-Smith & Macandza 2012) or breathing air in diving birds and mammals (Parkes *et al.* 2002; Hoskins, Costa & Arnould 2015). It can also be determined by external factors such as day length in diurnal species be they wild (Chapman, Chapman & McLaughlin 1989) or domestic (Squires 1976; Shrader et al. 2012).

Hedenstrom & Alerstam (1995) proposed a general model to predict the optimization of flight speed in birds during foraging which may apply to mammalian herbivores since the relationship between elephant travelling speed and energy consumption is known and follows similar allometric relationships (Langman et al. 1995). Interestingly, Hedenstrom & Alerstam (1995) predict flight speed decreases with distance between patches, as the average energetic gain decreases, whereas they predict flight speed increases with patch quality, as a result of greater energetic gains. Yet, we found elephant outgoing and returning speed increases with the distance to the foraging area and increased during the dry season (*Figure 51*). However, water dependence can explain this discrepancy. The model developed by Hedenstrom & Alerstam (1995) considers a single optimization currency, net energy intake, which allows an increase in total trip duration due to longer patch residence when distance to the foraging patch increases. Elephants may not afford to forage longer because of drinking constraints and must trade-off time spent travelling with time spent foraging.

In addition, depletion occurs around the central place. As a consequence, patch quality and distance from the central place are correlated (Birt et al. 1987; Rozen-Rechels et al. 2015). Thus, within Hedenstrom & Alerstam's model, the negative effects of patch distance could be outweighed by the positive effect of patch quality. Moreover, the higher average speed and steeper slope on return trips confirms elephants could be trying to stay as far away, as long as possible, to minimize missed opportunity costs similarly to other central place foraging herbivores (Shrader et al. 2012). Our results advocate for including measurements of

movement metrics that change the space-time properties of a trip such as speed and straightness in central place or multiple central place foraging models. Species such as larger herbivores and colonial seabirds or mammals with different minimum costs of transport and body sizes would be particularly good candidates to assess the importance of movement adjustments relative to foraging time and intake in response to central place depletion. However, such models would have to account for external factors such as winds and currents in marine animals or temperature in terrestrial mammals.

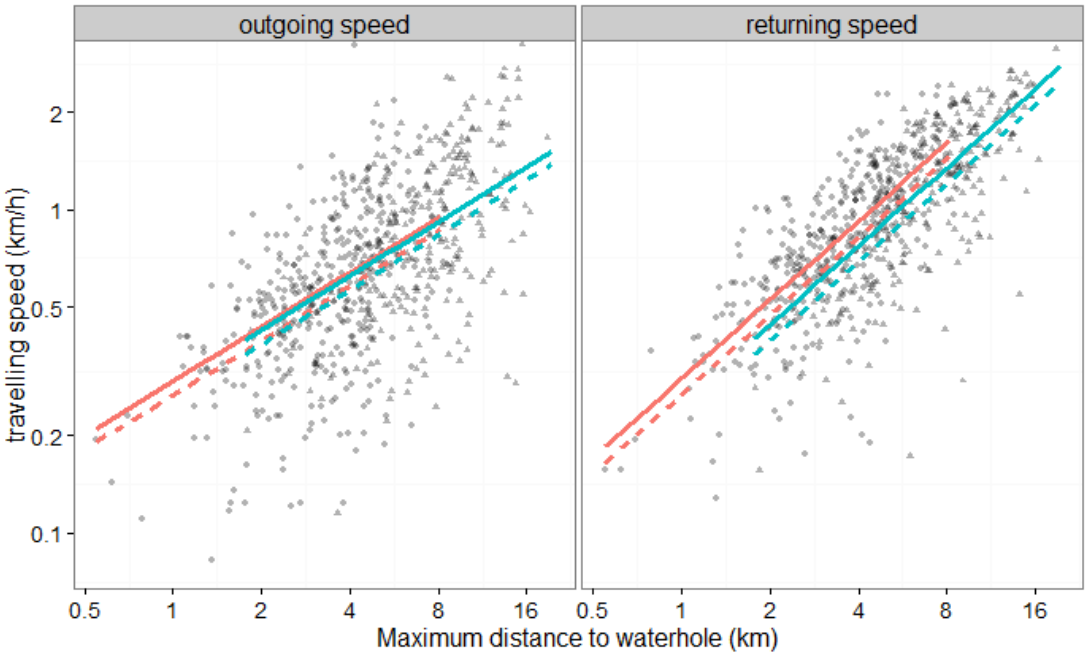


Figure 51: Travelling speed according to the maximum distance from the waterhole. Outgoing speed (left panel) and returning speed (right panel) during 24h trips (red) and 48h trips (blue). Mixed linear model estimates are shown for July 1st (dashed line) and October 1st (full line). Note the log-log relationship.

2.2 The importance of surface water as a central place

Central place foraging models generally consider the optimization of a single currency linked to the foraging resource. In the case of elephants, this currency switches from nitrogen maximization during the rainy season (i.e forage quality) to energy maximization during the dry season (i.e. forage quantity) (Pretorius et al. 2012). As the dry season advances, forage availability (and intake) strongly decrease close to water, in response to missed opportunity costs, central place foraging elephants are expected to travel further and spend more time away from water (Shrader et al. 2012). Elephant foraging behavior during looping trips is consistent with these predictions; elephants minimize the time spent in depleted areas close to water through directed movement at elevated speed (chapter 1) which enables them to select for areas away from waterholes at large and fine scales (chapter 2).

However, foraging constraints fall short of explaining key aspects of elephant movement patterns during the dry season, such as the increase in drinking frequency and the multiplicity

of trip durations. Water and forage are non-substitutable resources during the dry season. In addition to maximizing forage intake, elephants must also manage currencies associated with water intake such as thermoregulation and osmoregulation (Fuller et al. 2014). Thus, the constraints imposed by forage depletion on foraging distance and energy intake developed in the previous section can also be applied to water requirements. The greater frequency of visits to waterholes as the dry season advances is consistent with increasing water requirements for thermoregulation due to increasing ambient temperature (Dunkin et al. 2013). Furthermore, elephant preference to visit waterholes at dusk enables them to cool off by spraying and bathing upon arrival (Rowe et al. 2013; Dunkin et al. 2013) whereas during the outgoing trip the absence of solar radiative heat and lower temperatures allow elephants to dissipate excess heat (Rowe et al. 2013). It is necessary to consider both water and foraging constraints to explain the seasonal trends in elephant movement patterns. However, these patterns raise a question: Are elephant's choice to increase travel speed and optimize navigation unique to elephants?

2.3 Is walking faster a general response to central place trade-offs?

Elephant gigantic body size may be the leading factor explaining why they increase travelling speed during the dry season. Relative to their size, elephants can increase walking speed for a lower energetic cost than any other terrestrial mammalian species (Langman et al. 1995). However, they also have the highest total energetic requirements. As discussed previously, their large body size also makes them particularly sensitive to thermoregulatory constraints. To save water, smaller bodied species might opt for other behavioral strategies such as a reduction of their foraging intake (McFarlan & Wright 1969) or even a reduction of time spent travelling (Daws & Squires 1974). Indeed, smaller species may be much less constrained by water limitation and can accommodate a reduction of watering frequency by increasing the quantity of water ingested at each visit in order to forage further (Squires & Wilson 1971). Moreover, elephants spend 17-19h foraging during the dry season in an attempt to fulfill their energetic requirements (Moss, Croze & Lee 2011). Smaller herbivores spend less time foraging and more time resting (and ruminating for foregut fermenters) thus smaller species are more likely to reduce time spent resting than increasing their travel speed (Squires 1976).

Surface water availability shapes ecosystems and has probably played just as much of a role in the evolution and radiation of herbivores in Africa as the emergence of savanna grasslands (Derry & Dougill 2008). Each species combines an array of unique physiological, morphological and behavioral adaptations that allow them to exploit different water dependence niches (Redfern et al. 2003; Fuller et al. 2014). Elephants may have a greater propensity to increase travelling speed due to their higher thermoregulatory constraints and greater foraging time requirements. However, other species may be subjected to similar constraints when confronted with forage depletion. To avoid such confounding effects, a simple experiment on domestic livestock at different densities and at different seasons could be implemented to test the generality of the response to the drinking vs. forage depletion trade-off.

3 Depletion and landscape complementation effects of surface water

In savanna systems, large herbivore biomass increases with primary productivity which is itself correlated to rainfall (Fritz *et al.* 1994). Artificial water provisioning breaks this relationship by increasing the area available to herbivores during the dry season allowing herbivore densities to increase for similar rainfall and primary productivity (Illius & O'Connor 2000). A dense network of artificial water pans allows herbivore populations to increase during years of average or above average rainfall. During droughts, large herbivores seek refuge in these areas that become severely depleted. For example, extensive water provisioning in Klaserie Private Nature Reserve was identified as the main cause of the 90% die-off of large herbivores during a drought in 1981-1983 (Walker et al. 1987). In Kruger NP, where nearly the entire park was within 5km of surface water, changing management paradigm has led to water point closure over the last two decades (Gaylard, Owen-smith & Redfern 2003). Waterhole density in Hwange NP never reached the levels of Kruger. However, following a drop in water provisioning during the 2000-2010 decade new boreholes are being sunk and water point density is increasing, particularly in private concessions which may have several water pans within a few kilometers of one another. However, few studies have attempted to put individual foraging patterns in perspective with the effects of waterhole density on forage depletion.

In chapter 3, we found elephants avoided areas with high waterhole density at a scale of 5km to 7km. In other words, elephants avoid areas where water points are within 5-7 km of each other. Yet, elephants are nearly always within 10km from a waterhole and spend about 50% of their time between 2 km and 5 km from water during the dry season (chapter 1). These patterns are consistent with the first radio-tracking study conducted on elephants in Hwange, three decades ago, during the early 1980's, when the elephant population was barely half of what it is today (Conybeare 1991). This raises several questions:

(i) On the basis of Conybeare's and our data can we detect if elephants actually travel further? The patterns observed by Conybeare and our study are broadly similar and both study areas overlap extensively. However, confounding factors such as time of day, time of the year and yearly rainfall may be sufficient to mask significant differences of the same order than the increase of distance to water by about 1 km that we observed for 24h trips over the course of the dry season.

(ii) Is it worthwhile for elephants to travel further? Regardless of travelling costs, habitat availability scales quadratically and not linearly with distance to water. As a result, for similar durations spent at different distances to water, elephant impact is much higher close to water. As an elephant walks away from a water point, it has to decide whether to keep moving or slow down and forage: When the elephant is 1km from water, if it decides to go 1km further, the area of available habitat will quadruple. If the elephant asks itself the same question at 8km from water, the area of available habitat will only increase by 25%. Thus the marginal gain of travelling further decreases hyperbolically

(Figure 52). This simple geometric constraint suggests that even at low levels of depletion (i.e. in the 1980's) it may be highly advantageous to travel away from water at short distances to increase the area of available habitat. However, as distance to water increases this advantage becomes less apparent, especially if one considers the influence of other waterholes. As a result, even substantial differences in foraging distances similar to the ones we described in chapter 2 may be difficult to detect on the basis of a visual appraisal of figures from Conybeare's work.

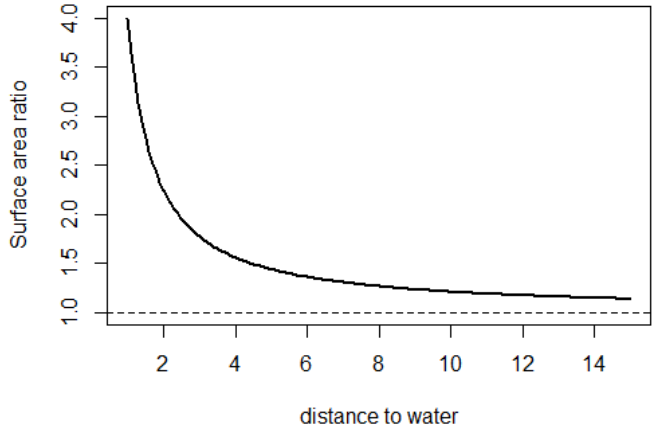


Figure 52: Theoretical marginal habitat gain. Although, the surface area increases quadratically with distance to water the marginal gain of going 1km further decreases hyperbolically.

Even though we cannot exclude that elephants do not range further than in the 1980's, our results consistently show avoidance by elephants of areas with high waterhole density during the dry season which we interpret as an effect of forage depletion. As an illustrative example of elephant's avoidance of high density areas, I overlapped two elephant dry season home-ranges with a waterhole density map estimated at a scale of 6km (Figure 53). The core dry season home-ranges of both migrant and resident elephants appear to be essentially located in areas with intermediate waterhole densities. Elephants avoid areas with waterholes within less than 5-7 km from each other (in red on Figure 53) but do not use areas beyond 10km from water (in blue on Figure 53).

Including waterhole density at the appropriate scale suggests relatively sparse waterhole provisioning might benefit elephants in the long run by reducing the proportion of their dry season home-range that is too close to water and heavily depleted. However, this scheme may not be applicable to other herbivore species and warrants a comprehensive habitat selection study in order to establish similar relations for other large herbivores. Such an approach would be particularly relevant for rare and less water dependent species such sable and roan antelope (*Hippotragus niger* and *Hippotragus equinus*) whose decline has been associated with water provisioning and attributed to direct and indirect competition with dominant grazers such as wildebeest and zebra (Harrington et al. 1999) or possibly elephants (Crosmary et al. 2015). Accordingly, sable and roan antelope drink less often (Cain, Owen-Smith &

Macandza 2012) and are expected to negatively respond to waterhole density at a larger scale than other herbivores. Contrasting the waterhole density maps at these respective scales would provide testable habitat suitability maps that could be confronted to animal densities in the field.

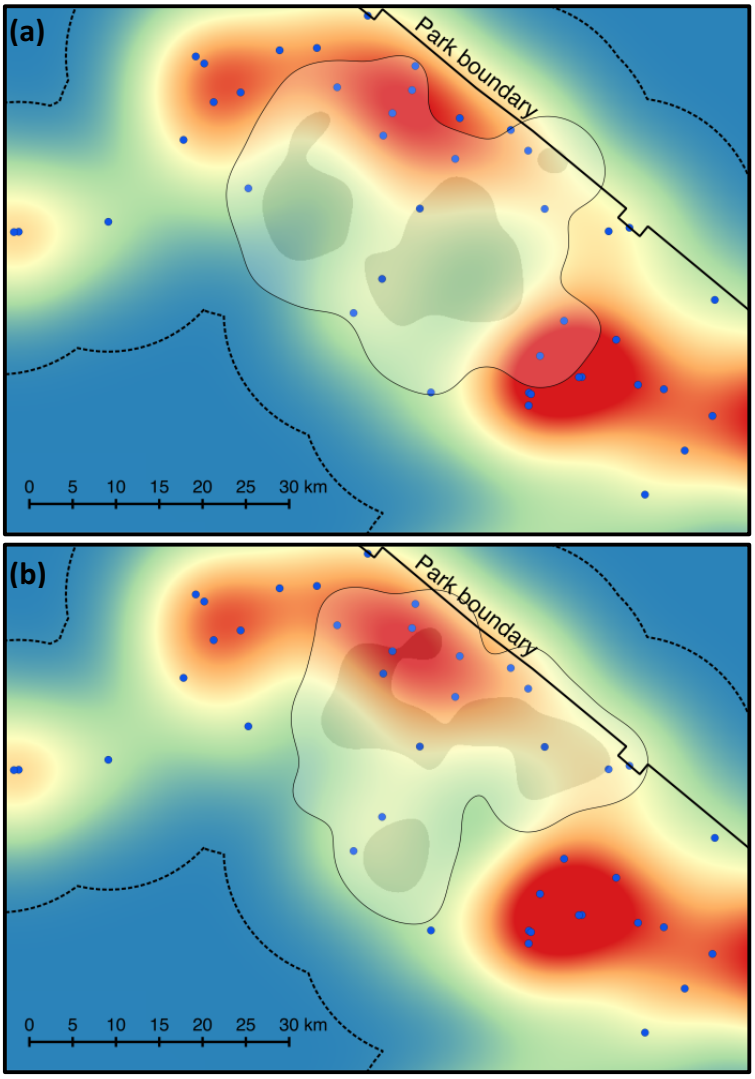


Figure 53: Dry season home-range according to waterhole density. The core home-range is shown in grey (50% Utilization Distribution) and the total range in white (95% UD) for a migrant (a) and a resident individual (b). Waterholes are represented by blue points. A waterhole density function (smoothing factor = 6km) is shown in the background. The dashed line is at 15km from water.

Overall, we found that in a semi-arid ecosystem structured by punctuated water sources, foraging decisions and habitat selection reflected forage depletion close to water rather than landscape complementation. This pattern may not hold for other types of water sources such as rivers or lakes that are associated with large riparian areas or floodplains. More widespread water distribution in conjunction with greater intrinsic habitat quality close to water due to potential regrowth would strengthen the effect of complementation.

4 The future of surface water provisioning as a management tool?

4.1 Current water management policies in Hwange NP

Artificial water provisioning has been the backbone of Hwange NP management policies since its proclamation (Davison 1967; Cumming 1981; Chamaillé-Jammes *et al.* 2014). As a result of pumping, 60-70% of Hwange NP remains within 10km of a perennial water source during the dry season. In the absence of pumping, this figure would drop to less than 30% in dry years, 50% on average years and remain at 60-70% on years with above average rainfall (Chamaillé-Jammes, Fritz & Murindagomo 2007b). Current pumping efforts are shared between Zimbabwe Parks and Wildlife Management Authority, private tourism concessions and an NGO (Friends of Hwange). During the course of my PhD, game water supply was in a state of permanent crisis; undermanned, underfunded and relying on obsolete equipment. As a result, pumping effort management is currently dictated by economic rather than ecological priorities. Waterholes that provide the best game viewing opportunities are maintained in priority. Over the past few years new boreholes have been sunk in the vicinity of private concessions. The more popular and accessible water pans (e.g. Guvalala & Nyamandhlovu Figure 54, pers. obs.) have a more reliable water supply than the more isolated water pans that are the first ones sacrificed in times of fuel shortage and are less likely to be repaired rapidly if breakdowns occur (e.g. Manga 1 Figure 54). The landscape of water supply in Hwange is shifting from a historical attempt to spread out the water supply and increase the dry season home-range of herbivores to islands of high waterhole density in areas visited by tourists. On the basis of the knowledge I have acquired on elephant movement patterns and my personal observations in the field, I fear these trends might reduce the ability of the Hwange socio-ecosystem to meet the challenges of wildlife conservation in a context of aridification.

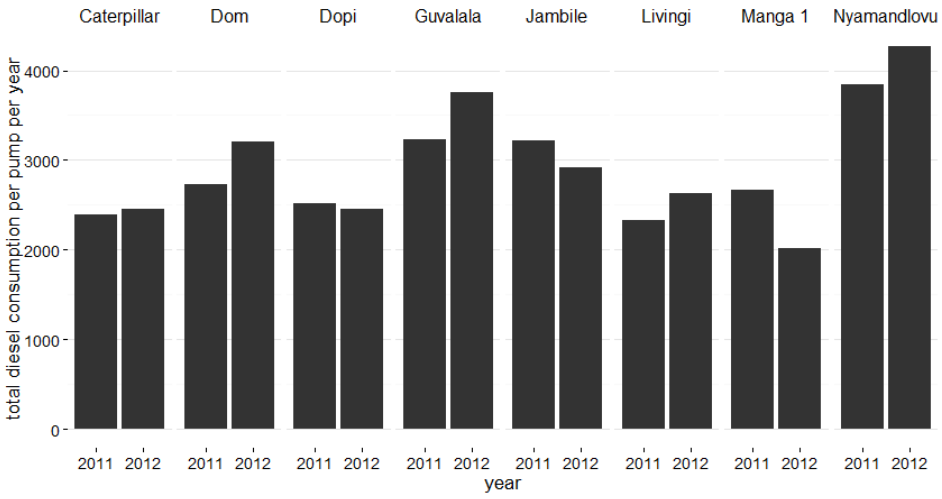


Figure 54: The cost of pumping: Fuel consumption (in L, diesel) by pumps maintained by Zimbabwe Parks and Wildlife Management Authority, over two years with below average rainfall.

4.2 Local and regional aridification trends

The aridification of Southern Africa is already affecting Hwange NP (Chamaillé-Jammes, Fritz & Murindagomo 2007a) and expected to worsen over the region during the 21st century (Giannini et al. 2008). Rather than a decrease in average precipitation, inter-annual variability has risen in a highly variable environments, increasing the frequency and severity of droughts (Fauchereau *et al.* 2003; Chamaillé-Jammes, Fritz & Murindagomo 2007a). Droughts are periods with below average rainfall which result in lower forage availability (Chamaille-Jammes, Fritz & Murindagomo 2006) and an advanced dry-up of waterholes (chapter 1). In Hwange NP, Dudley (2000) reported the duration of the rainy season rather than total annual precipitation was the best predictor of elephant mortality. Thus, droughts can result from the combined effects of lower yearly precipitation and a longer duration of the dry season when the rains come too late or end too early.

4.3 The effect of artificial water provisioning on wildlife

4.3.1 Artificial water provisioning and sensitivity to drought

During years of lower rainfall, elephant numbers at waterholes increase earlier on in the dry season and reach higher numbers (Valeix 2011, box 4). These patterns could result from higher aggregation of local populations but probably reflect changes in the overall migration pattern (chapter 1). Migratory elephants returned to their dry season home-range between 1 and 2 months later in 2014 (above average rainfall) than 2013 (average rainfall) presumably due to the persistence of surface water in their rainy season home-range. Partial elephant migration ahead of time may thus amplify the effects of drought on resource depletion in the dry season home-range. As a result of aggregation, areas with higher waterhole densities also harbor higher elephant densities. However, elephant densities increase asymptotically with waterhole density (Chamaillé-Jammes, Valeix & Fritz 2007). In addition Chamaillé-Jammes *et al.* (2008) found aggregation levels were lower in dry years, suggesting that elephant numbers increase more at less crowded waterholes. The tendency to spread out when surface water becomes scarce is consistent with habitat selection patterns reported in chapter 3, suggesting elephants shift towards low waterhole density areas to avoid the effects of forage depletion (Figure 53). Moreover, we found elephants respond to waterhole density at a scale of 5-7 km. Pumped water pans around lodges fall within that range and potentially increase the effect of resource depletion. In the advent of a drought, we would therefore expect elephants (and other herbivore species) using these areas to be at higher risk of mortality (Walker et al. 1987).

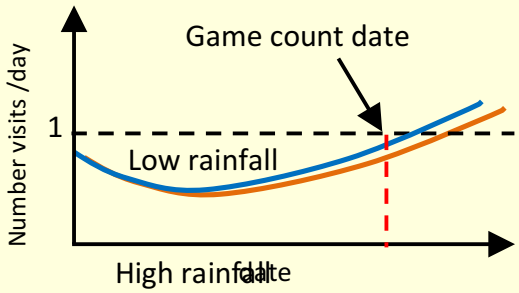
Our analysis of elephant movement in chapter 2 sheds light on the underlying process of resource limitation for elephants: As the dry season progresses, elephants increase their drinking frequency, distance to water and travelling speed. Elephants increase energetic expenditure and possibly exposure to thermoregulatory stress. In our study, this increase was suddenly halted by an early rainfall event that disrupted elephant movement patterns (elephants immediately moved to the area where it had rained and stopped visiting known

perennial water pans). It is uncertain whether the trend in increasing speed and distance during 24h trip would continue until the values become similar to 48h long trips. However, we previously concluded trip speed and perhaps distance may not increase beyond these values due to the limited movement abilities of elephant calves (chapter 2). Calf mortality during drought would result from elephant family herds having to travel at higher speeds and cover larger distances to fulfill their energetic and water requirements.

Box 4: Surface water use and wildlife monitoring

An accurate knowledge of population abundance and distribution is paramount for both managers and researchers. Large mammal populations in Hwange NP are estimated annually by a standardized waterhole counts over a period of 24h. Waterhole counts cover all water dependent species, are relatively easy to implement, less costly than road counts or aerial counts. These counts are currently conducted by volunteers affiliated to Wildlife & Environment Zimbabwe (WEZ). However, the total number of animals counted is negatively correlated to annual rainfall (Chamaillé-Jammes et al. 2008). The influence of rainfall can be accounted for by comparing waterhole counts to aerial counts (Valeix et al. 2008b). Information obtained from GPS data can be used to correct the bias incurred by partial migration and drinking frequency on population estimates by waterhole counts:

- During years with higher rainfall, elephants return from their rainy season home-range later in the dry season and may not return to their dry season home-range altogether. Waterhole counts are conducted in September, long after most migrants have returned and they are preceded by an aerial survey of all known water sources in the park to maximize counting effort. Inter-annual variability in migration patterns are thus unlikely to substantially affect population estimates given by systematic waterhole counts.
- Waterhole counts rely on the assumption that animals come to drink once a day. However, we found elephant drinking frequency varies nearly twofold for during the dry season (chapter2). The weekly distribution of trip durations can be used to simulate the proportion of groups that did not come and the ones that were counted several times.



- However, drinking frequency at a same date may change according to inter-annual rainfall variability (as imagined in the graph above) due to greater water requirements (low forage water content) or higher uncertainty on the reliability of the water supply.
- Typical drinking frequency appears to vary substantially between sites, calling for site specific corrections. For instance elephants in Kruger NP prefer to drink at midday, do not have multiple trip periods and come to water on average every 18h (Thaker & Vanak pers. comm.) and Namib desert elephants may spend up to 4 days without drinking (Leggett 2006b).

Elephant arrival times at waterholes might be another indicator of increasing travelling constraints (Appendix II, chapter 2). Indeed the well-marked peaks at 5h, 24h, 48h and 72h tend to spread out during the dry season, suggesting elephants lose their ability to fine tune trip duration as the dry season advances. Interestingly, Polansky *et al.* (2013) found subordinate individuals spent more energy and had lower movement autocorrelation than dominant individuals during the dry season. Speed and distance travelled as well as movement periodicity can serve as indicators of resource stress. Recent works have pointed out that animals under resource limitation were unable to maintain physiological homeostasis (Hetem *et al.* 2014). These conclusions may be expanded to behavioral (and movement) homeostasis suggesting that individuals under stress will be unable to maintain their circadian rhythms and exhibit greater variability in their movement rates. Greater daily displacement and expanding ranges appeared to be the norm rather than the exception among savanna ungulates during the dry season. Collared zebra, buffalo and cattle had less predictable movement patterns and greater movement rates at the end of the dry season. The analysis of elephant movement revealed the mechanism underlying the effects of depletion at the individual scale. Analyses of key movement components such as speed, travel distance and periodicity provide behavioral indicators of resource limitation. The next step is to effectively link these parameters to individual fitness and use them to assess resource availability from the animal's perspective.

Water provisioning may provide an effective management tool to mitigate the effects of drought by maintaining a substantial part of the park accessible to herbivores (Chamaillé-Jammes, Fritz & Murindagomo 2007b). The buffering effect of waterholes could be enhanced by pumping some waterholes in areas with low depletion only during periods of drought to provide additional forage. However, current water provisioning practices are less likely to provide this buffering effect as in the past due to greater areas with high waterhole densities that become heavily depleted in times of drought (Walker *et al.* 1987).

4.3.2 Edge effects of artificial water provisioning

Hwange National Park has historically been severed from the Zambezi and Gwayi river catchments (Figure 55). Water provisioning has provided an alternative for wildlife to remain in Hwange NP throughout the dry season. Recent conservation initiatives such as reconnecting Hwange NP with the Zambezi valley through the Hwange Sanyati Biological Corridor pose a number of coexistence challenges if, as expected, large mammals effectively use the corridor to access these perennial rivers. Our study of elephant and buffalo movement patterns according to cattle presence in Sikumi Forest (chapter 4) provides a case study by which we quantified the edge effects and described the role of surface water on coexistence between wildlife and domestic livestock.

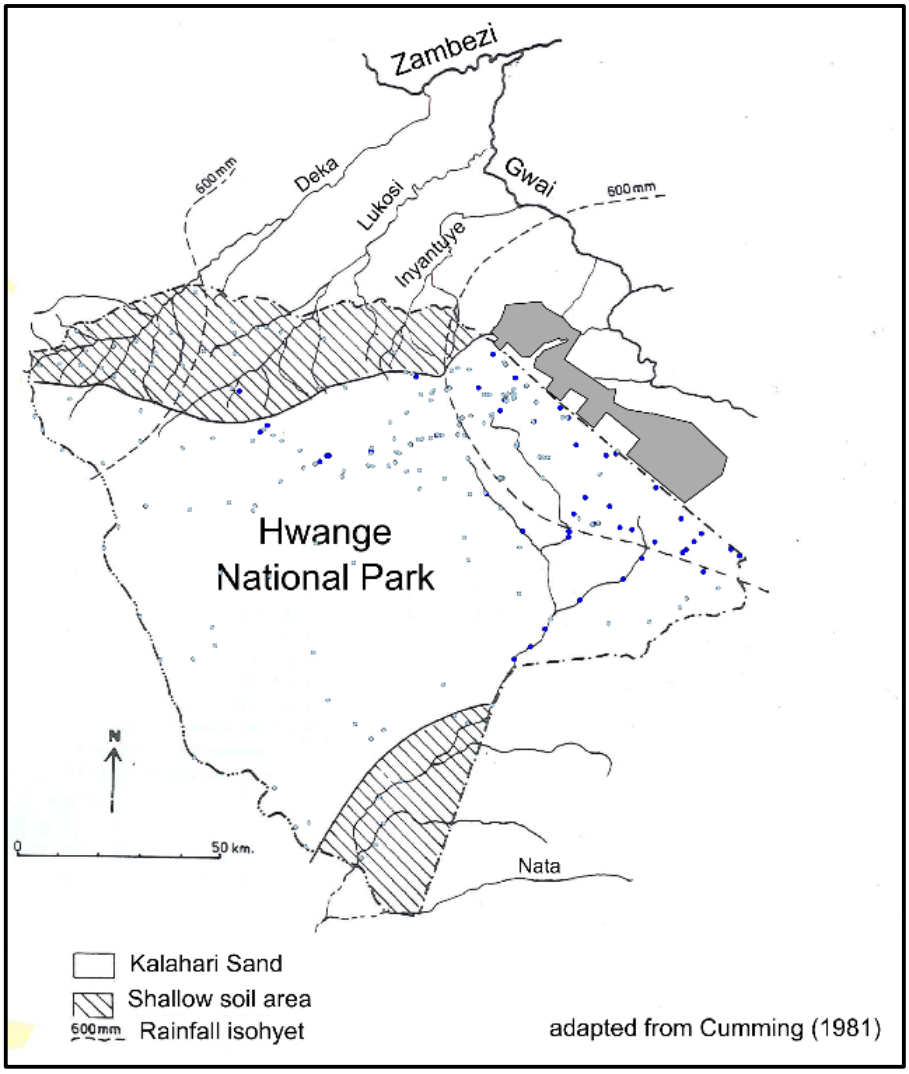


Figure 55: Perennial rivers around Hwange NP and Sikumi Forest.

We found elephant and buffalo strongly avoid cattle at the boundary of Sikumi Forest. Buffalo always remained within the protected area whereas elephant would make rare excursions into the communal land and return to Sikumi Forest east to the Gwayi river catchment. Widespread water availability during the rainy season gave rise to spatial partitioning. Cattle drink at natural water pans within the first kilometers of the boundary and graze in their vicinity whereas buffalo and elephant use water sources further inside Sikumi Forest. Although their diets overlap extensively during the rainy season (Prins 2000; Kartzinel *et al.* 2015) wild and domestic herbivores coexist at the boundary of Sikumi Forest through spatial partitioning (Sitters *et al.* 2009). However, as surface water becomes scarce the fate of domestic and wild herbivores differ. Cattle obtain drinking water from boreholes at their home-kraals which allows them to graze freely, far away from the dried up water pans, but within the constraints of the central place effects of their home-kraal. Conversely, wild herbivores remain closer to artificial water pans provided by safari operators. The location of these permanent water pans determines the outcome of cattle – wildlife interactions. Avoidance of cattle by wildlife promotes coexistence during the rainy season when the

presence of cattle probably acts as a buffer and reduces wildlife excursions in fields in the communal land. However, during the dry season, artificial water provisioning close to the boundary attracts wildlife that no longer have the ability to avoid domestic livestock. Furthermore, domestic livestock can easily reach these pans and may attempt to come and drink. The presence of livestock is a source of conflict between tourism operators and cattle owners. For cattle owners, water provisioning close to the boundary also increases the negative effects of close encounters with wildlife such as disease transmission (Miguel *et al.* 2013) or livestock depredation (Kuiper *et al.* 2015).

Artificial water provisioning may be necessary to restore a functional corridor between the Gwayi and Zambezi river catchments and Hwange National Park. However the locations of these water sources should be picked with care to minimize conflict with people living in the area. Incentives to bolster cattle husbandry by encouraging communal herding may also be advantageous by promoting spatial partitioning between livestock and wildlife. Particular attention is needed in years of drought. The 1994 drought was the primary reason why cattle were allowed to enter the Forestry land following substantial livestock losses. Cattle are less expected to suffer from water scarcity due to the presence of boreholes in the communal land, however they may be under severe intraspecific competition leading them to make greater incursions into the protected area (Butt 2014). Equally, elephants may be under greater pressure inside protected areas to come out in search of forage. Allowing elephants and other herbivores to migrate further towards permanent rivers may partially alleviate Hwange NP, however additional pumping inside protected areas during droughts could also reduce the pressure on boundary areas.

5 Studying animal movement to inform water provisioning policies in arid rangelands

In arid and semi-arid ecosystems, water is a key limiting resource due to the spatial and temporal constraints it exerts on organisms. People have drastically modified this constraint through widespread water provisioning in arid rangelands. The numerical response, characterized by the increase in herbivore abundance and the development of piospheres, has been well documented, yet information at the individual level remains surprisingly scant.

In order to assess the influence of surface water, it is necessary to distinguish time allocated to water provisioning from other activities. In the case of elephants, this distinction enabled the identification of foraging trips as the most pertinent unit to analyse the spatial-temporal trade-offs between foraging and drinking. To do so, we established a dynamic map that accurately mapped changes in water availability in time and space. However, the location of key resources may not be known and may need preliminary recursion analyses to identify them (Benhamou & Riotte-Lambert 2012). Field validation of water availability and waterhole use was a key step to give reliable estimates of water dependence.

Throughout this thesis I analysed the landscape effects of surface water distribution on foraging behaviour within the central place – landscape complementation continuum. Central place effects dominate when waterholes are isolated, multiple central place effects appear when an individual can utilise several water points and landscape complementation becomes a more appropriate framework when water distribution becomes widespread or when larger scales are considered. The application of this framework revealed surface water distribution was a strong constraint on elephants at multiple scales. It's application to other African herbivores could provide the first quantification of the role of surface water in the evolution of herbivores (Derry & Dougill 2008) and give practical tools to design water provisioning schemes for wildlife or free ranging livestock.

Water dependence is generally considered as a dry season constraint, however we found rainy season surface water distribution played an important role in the movement patterns of three species of herbivores throughout the year. In the long run, arid ecosystems have become organised around surface water through major processes such as trophic relationships (herbivory, parasitism and predation) and nutrient cycling as well. Acknowledging the importance of surface water in multiple processes implies greater attention must be given to its role during the rainy season when most of us still believe it is not a constraint.

Acknowledgements

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References

Adams, R. a. & Hayes, M. a. (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, **77**, 1115–1121.

Adler, P.B. & Hall, S. a. (2005) The development of forage production and utilization gradients around livestock watering points. *Landscape Ecology*, **20**, 319–333.

Adriansen, H. & Nielsen, T. (2002) Going where the grass is greener: on the study of pastoral mobility in Ferlo, Senegal. *Human Ecology*, **30**, 215–226.

Atickem, A. & Loe, L.E. (2014) Livestock-wildlife conflicts in the Ethiopian highlands: Assessing the dietary and spatial overlap between mountain nyala and cattle. *African Journal of Ecology*, **52**, 343–351.

Aublet, J.-F., Festa-Bianchet, M., Bergero, D. & Bassano, B. (2009) Temperature constraints on foraging behaviour of male Alpine ibex (Capra ibex) in summer. *Oecologia*, **159**, 237–47.

Augustine, D.J. & Springer, T.L. (2013) Competition and facilitation between a native and a domestic herbivore: Trade-offs between forage quantity and quality. *Ecological Applications*, **23**, 850–863.

Bailey, D.W., Gross, J.E., Laca, E. a., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, **49**, 386–400.

Barraquand, F. & Benhamou, S. (2008) Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology*, **89**, 3336–3348.

Bartlam-Brooks, H.L. a, Beck, P.S. a, Bohrer, G. & Harris, S. (2013) In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *Journal of Geophysical Research: Biogeosciences*, **118**, 1427–1437.

Basille, M. (2015) hab: Habitat and movement functions.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*.

Bauer, S., Nolet, B.A., Giske, J., Chapman, J.W., Åkesson, S., Hedenström, A. & Fryxell, J.M. (2011) Cues and decision rules in animal migration. *Animal Migration: A Synthesis* (eds E.J. Milner-Gulland),, J.M. Fryxell), & A.R.E. Sinclair), pp. 68–87. Oxford University Press.

De Beer, Y. & Van Aarde, R. (2008) Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments*, **72**, 2017–2025.

De Beer, Y., Kilian, W., Versfeld, W. & Van Aarde, R. (2006) Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments*, **64**, 412–421.

van Beest, F.M., Van Moorter, B. & Milner, J.M. (2012) Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour*, **84**, 723–735.

van Beest, F.M., Mysterud, A., Loe, L.E. & Milner, J.M. (2010) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *The Journal of animal ecology*, **79**, 910–22.

Ben-Shahar, R. (1993) Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*, **65**, 249–256.

Benhamou, S. (2011) Dynamic approach to space and habitat use based on biased random bridges. *PloS one*, **6**, e14592.

Benhamou, S. (2013) Of scales and stationarity in animal movements. *Ecology letters*, 261–272.

Benhamou, S. & Riotte-Lambert, L. (2012) Beyond the Utilization Distribution: Identifying home range areas that are intensively exploited or repeatedly visited. *Ecological Modelling*, **227**, 112–116.

Bennitt, E., Bonyongo, M.C. & Harris, S. (2014) Habitat Selection by African Buffalo (Syncerus caffer) in Response to Landscape-Level Fluctuations in Water Availability on Two Temporal Scales. *PloS one*, **9**, e101346.

Bergman, C.M., Fryxell, J.M., Gates, C.C. & Fortin, D. (2001) Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology*, **70**, 289–300.

Birkett, P.J., Vanak, A.T., Muggeo, V.M.R., Ferreira, S.M. & Slotow, R. (2012) Animal perception of seasonal thresholds: changes in elephant movement in relation to rainfall patterns. *PloS one*, **7**, e38363.

Birt, V., Birt, T., Goulet, D., Cairns, D. & Montevecchi, W. (1987) Ashmole's halo: direct evidence for prey depletion by a seabird . *Marine Ecology Progress Series*, **40**, 205–208.

Blanc, J.J., Barnes, R.F.W., Craig, J.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. & Hart, J.A. (2007) *African Elephant Status Report 2007. An Update from the African Elephant Database.* Gland, Switzerland.

Bohrer, G., Beck, P.S., Ngene, S.M., Skidmore, A.K. & Douglas-Hamilton, I. (2014) Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. *Movement Ecology*, **2**, 2.

Bonenfant, C., Gaillard, J.-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. (2009) Empirical Evidence of Density-Dependence in Populations of Large Herbivores. *Advances in Ecological Research* pp. 313–357.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Brooks, C.J. & Harris, S. (2008) Directed movement and orientation across a large natural landscape by zebras, Equus burchelli antiquorum. *Animal Behaviour*, **76**, 277–285.

Brown, J.S. (1988) Patch use as an indication of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, **22**, 37–47 ST – Patch use as an indication of habitat.

Butt, B. (2010) Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. *Journal of Arid Environments*, **74**, 403–413.

Butt, B. (2011) Coping with Uncertainty and Variability: The Influence of Protected Areas on Pastoral Herding Strategies in East Africa. *Human Ecology*, **39**, 289–307.

Butt, B. (2014) the Political Ecology of 'Incursions': Livestock, Protected Areas and Socio-Ecological Dynamics in the Mara Region of Kenya. *Africa*, **84**, 614–637.

Byrne, R.W., Noser, R., Bates, L.A. & Jupp, P.E. (2009) How did they get here from there ? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, **77**, 619–631.

Cain, J.W., Owen-Smith, N. & Macandza, V. a. (2012) The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology*, **286**, 58–67.

Cerling, T.E., Wittemyer, G., Ehleringer, J.R., Remien, C.H. & Douglas-Hamilton, I. (2009) History of Animals using Isotope Records (HAIR): a 6-year dietary history of one family of African elephants. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 8093–100.

Cerling, T.E., Wittemyer, G., Rasmussen, H.B., Vollrath, F., Cerling, C.E., Robinson, T.J. & Douglas-Hamilton, I. (2006) Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 371.

Chamaillé-Jammes, S., Fritz, H. & Holdo, R.M. (2007) Spatial relationship between elephant and sodium concentration of water disappears as density increases in Hwange National Park, Zimbabwe. *J. Trop. Ecol.*, **23**, 725–728.

Chamaillé-Jammes, S., Fritz, H. & Madzikanda, H. (2009) Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. *Ecography*, **32**, 871–880.

Chamaille-Jammes, S., Fritz, H. & Murindagomo, F. (2006) Spatial patterns of the NDVI–rainfall relationship at

the seasonal and interannual time scales in an African savanna. *International Journal of Remote Sensing*, **27**, 5185–5200.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007a) Detecting climate changes of concern in highly variable environments: Quantile regressions reveal that droughts worsen in Hwange National Park, Zimbabwe. *Journal of Arid Environments*, **71**, 321–326.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007b) Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: Potential implication for herbivore dynamics. *Austral Ecology*, **32**, 740–748.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. & Clobert, J. (2008) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *The Journal of animal ecology*, **77**, 135–44.

Chamaillé-Jammes, S., Mtare, G., Makuwe, E. & Fritz, H. (2013) African elephants adjust speed in response to surface-water constraint on foraging during the dry-season. *PloS one*, **8**, e59164.

Chamaillé-Jammes, S., Valeix, M. & Fritz, H. (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *J Appl Ecology*, **44**, 625–633.

Chamaillé-Jammes, S., Valeix, M., Madzikanda, H. & Fritz, H. (2014) Surface Water and Elephant Ecology: Lessons from a Waterhole-Driven Ecosystem, Hwange National Park, Zimbabwe. *Elephants and Savanna Woodland Ecosystems* (eds C. Skarpe),, J.T. du Toit), & S.R. Moe), pp. 118–131. Zoological Society of London.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-A. (2011) The ecology and evolution of partial migration. *Oikos*, **120**, 1764–1775.

Chapman, C. a., Chapman, L.J. & McLaughlin, R.L. (1989) Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*, **79**, 506–511.

Charnov, E.L. (1976) Optimal Foraging, the Marginal Value Theorem. *Theoretical population biology*, **9**, 129–136.

Choquenot, D. & Ruscoe, W. a. (2003) Landscape complementation and food limitation of large herbivores: habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology*, **72**, 14–26.

Conybeare, A.M. (1991) *Elephant Occupancy and Vegetation Change in Relation to Artificial Water Points in a Kalahari Sand Area of Hwange National Park*. University of Zimbabwe.

Conybeare, a. & Haynes, G. (1984) Observations on elephant mortality and bones in water holes. *Quaternary Research*, **22**, 189–200.

Cooper, S.M., Perotto-Baldivieso, H.L., Owens, M.K., Meek, M.G. & Figueroa-Pagán, M. (2008) Distribution and interaction of white-tailed deer and cattle in a semi-arid grazing system. *Agriculture, Ecosystems & Environment*, **127**, 85–92.

Cooper, S.M., Scott, H.M., de la Garza, G.R., Deck, A.L. & Cathey, J.C. (2010) Distribution and interspecies contact of feral Swine and cattle on rangeland in South Texas: implications for disease transmission. *Journal of wildlife diseases*, **46**, 152–64.

Coppolillo, P.B. (2001) Central-Place Analysis and Modeling of Landscape -Scale Resource Use in an East African Agropastoral System. *Landscape Ecology*, 205–219.

Cornélis, D., Benhamou, S., Janeau, G., Morellet, N., Ouedraogo, M. & de Visscher, M.-N. (2011) Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes. *Journal of Mammalogy*, **92**, 1287–1297.

Courbin, N., Fortin, D., Dussault, C. & Courtois, R. (2009) Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecology*, **24**, 1375–1388.

Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E. & Chamaillé-Jammes, S. (2015) Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*.

Craiu, R. V., Duchesne, T. & Fortin, D. (2008) Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal*, **50**, 97–109.

Craiu, R. V., Duchesne, T., Fortin, D. & Baillargeon, S. (2011) Conditional Logistic Regression With Longitudinal Follow-up and Individual-Level Random Coefficients: A Stable and Efficient Two-Step Estimation Method. *Journal of Computational and Graphical Statistics*, **20**, 767–784.

Crosmary, W.-G., Chamaillé-Jammes, S., Mtare, G., Fritz, H., Côté, S.D., Chamaill, S., Mtare, G. & Steeve, D.C. (2015) Decline of sable antelope in one of its key conservation areas : the greater Hwange ecosystem , Zimbabwe. *African Journal of Ecology*, doi: 10.1111/aje.12207.

Crosmary, W.-G., Makumbe, P., Côté, S.D. & Fritz, H. (2012a) Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. *Animal Behaviour*, **83**, 1367–1376.

Crosmary, W.-G., Valeix, M., Fritz, H., Madzikanda, H. & Côté, S.D. (2012b) African ungulates and their drinking problems : hunting and predation risks constrain access to water. *Animal Behaviour*, **83**, 145–153.

Cross, P.C., Lloyd-Smith, J.O. & Getz, W.M. (2005) Disentangling association patterns in fission–fusion societies using African buffalo as an example. *Animal Behaviour*, **69**, 499–506.

Cumming, D.H.M. (1981) The management of elephant and other large mammals in Zimbabwe. *Problems in Management of Locally Abundant Wild Mammals.* pp. 91–118. Academic Press.

Cumming, D.H.M., Osofsky, S.A., Atkinson, S.J. & Atkinson, M.W. (2015) Beyond Fences : Wildlife , Livestock and Land Use in Southern Africa. *One health: The theory and practice of integrated health approaches* (eds J. Zinsstag),, E. Schelling),, D. Waltner-Toews),, M. Whittaker), & M. Tanner), pp. 243–257. C. A. B. International.

Cushman, S. a., Chase, M. & Griffin, C. (2005) Elephants in space and time. *Oikos*, **109**, 331–341.

Cushman, S.A., Chase, M. & Griffin, C. (2010) Mapping Landscape Resistance to Identify Corridors and Barriers for Elephant Movement in Southern Africa. *Spatial Complexity, Informatics, and Wildlife Conservation* pp. 193–221.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2013) Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PloS one*, **8**, e55182.

Davison, E. (1930) *Report on Wankie Game Reserve October, 1928 - March, 1930*.

Davison, E. (1967) *Wankie, The Story of A Great Gamer Reserve*, 3rd Editio. Thorntree Press, Bulawayo, Zimbabwe.

Daws, G.T. & Squires, V.R. (1974) Observations on the effects of temperature and distance to water on the behaviour of Merino and Border Leicester sheep. *The Journal of Agricultural Science*, **82**, 383.

Derry, J.F. & Dougill, A.J. (2008) Water location, piospheres and a review of evolution in African ruminants. *African Journal of Range & Forage Science*, **25**, 79–92.

Dohna, H.Z., Peck, D.E., Johnson, B.K., Reeves, A. & Schumaker, B. a. (2014) Wildlife-livestock interactions in a western rangeland setting: Quantifying disease-relevant contacts. *Preventive Veterinary Medicine*, **113**, 447–456.

Duchesne, T., Fortin, D. & Courbin, N. (2010) Mixed conditional logistic regression for habitat selection studies. *The Journal of animal ecology*, **79**, 548–55.

Dudley, J.P. (2000) Seed Dispersal by Elephants in Semiarid Woodland Habitats of Hwange National Park, Zimbabwe. *Biotropica*, **32**, 556–561.

Dudley, J. & Criag, G. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of …*, **39**, 187–194.

Duncan, C., Chauvenet, A.L.M., McRae, L.M. & Pettorelli, N. (2012) Predicting the future impact of droughts on

ungulate populations in arid and semi-arid environments. *PloS one*, **7**, e51490.

Dunham, K. (2015) *Aerial Survey of Elephants and Other Large Herbivores in Northwest Matabeleland (Zimbabwe) 2014*.

Dunkin, R.C., Wilson, D., Way, N., Johnson, K. & Williams, T.M. (2013) Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution. *The Journal of experimental biology*, **216**, 2939–52.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, 169–175.

Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L. & Davoren, G.K. (2009) Central-place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk*, **126**, 613–625.

Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, **6**, 439–447.

Fauchereau, N., Trzaska, S., Rouault, M. & Richard, Y. (2003) Rainfall variability and changes in Southern Africa during the 20th century in the global warming context. *Natural Hazards*, **29**, 139–154.

Ferguson, K. & Hanks, J. (eds). (2010) *Fencing Impacts: A Review of the Environmental, Social and Economic Impacts of Game and Veterinary Fencing in Africa with Particular Reference to the Great Limpopo and Kavango-Zambezi Transfrontier Conservation Areas*.

Forester, J.D., Im, H.K. & Rathouz, P.J. (2009) Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology*, **90**, 3554–3565.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Fortin, D., Buono, P.-L., Fortin, A., Courbin, N., Tye Gingras, C., Moorcroft, P.R., Courtois, R. & Dussault, C. (2013) Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. *The American naturalist*, **181**, 827–36.

Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009) Group-Size-Mediated Habitat Selection and Group Fission-Fusion Dynamics fo Bison under Predation Risk. *Ecology*, **90**, 2480–2490.

Fritz, H., Duncan, P., Curie, P., Sup, V., Clvrs, F. & The, F. (1994) On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **256**, 77–82.

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M. & Clobert, J. (2011) A food web perspective on large herbivore community limitation. *Ecography*, **34**, 196–202.

Fuller, A., Hetem, R.S., Maloney, S.K. & Mitchell, D. (2014) Adaptation to Heat and Water Shortage in Large, Arid-Zone Mammals. *Physiology*, **29**, 159–167.

Fullman, T. & Bunting, E. (2014) Analyzing Vegetation Change in an Elephant-Impacted Landscape Using the Moving Standard Deviation Index. *Land*, **3**, 74–104.

Fullman, T. & Child, B. (2013) Water distribution at local and landscape scales affects tree utilization by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, 1–9.

Gaidet, N. & Lecomte, P. (2013) Benefits of migration in a partially-migratory tropical ungulate. *BMC ecology*, **13**, 36.

Garstang, M., Davis, R.E., Leggett, K., Frauenfeld, O.W., Greco, S., Zipser, E. & Peterson, M. (2014) Response of African Elephants (Loxodonta africana) to Seasonal Changes in Rainfall. *PloS one*, **9**, e108736.

Gaston, A.J., Ydenberg, R.C. & Smith, G.E.J. (2007) Ashmole ' S Halo and Population Regulation in Seabirds. *Marine Ornithology*, 119–126.

Gaugris, J. & Rooyen, M. Van. (2010) Effects of water dependence on the utilization pattern of woody vegetation

by elephants in the Tembe Elephant Park, Maputaland, South Africa. *African journal of ecology*, 126–134.

Gaylard, A., Owen-smith, N. & Redfern, J. (2003) Surface water availability: implications for heterogeneity and ecosystem processes. *Kruger experience: ecology and management of savanna heterogeneity* (eds J.T. du Toit),, K.H. Rogers), & H.C. Biggs), pp. 171–188. Island Press, Washington.

Giannini, A., Biasutti, M., Held, I.M. & Sobel, A.H. (2008) A global perspective on African climate. *Climatic Change*, **90**, 359–383.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006) Application of random effects to the study of resource selection by animals. *J Anim Ecology*, **75**, 887–898.

Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, **12**, 445–455.

Guerbois, C. (2012) Considérer les aires protégées dans la dynamique des systèmes socio-écologiques pour une conservation intégrée et durable de la faune sauvage africaine. , 394.

Guerbois, C., Chapanda, E. & Fritz, H. (2012) Combining multi-scale socio-ecological approaches to understand the susceptibility of subsistence farmers to elephant crop raiding on the edge of a protected area. *Journal of Applied Ecology*, **49**, 1149–1158.

Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R. & Funston, P. (1999) Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, **90**, 69–78.

Harris, G.M., Russell, G.J., Aarde, R.I. Van & Pimm, S.L. (2008) Rules of habitat use by elephants Loxodonta africana in southern Africa: insights for regional management. *ORX*, **42**, 66–75.

Hayward, M.W. & Hayward, M.D. (2012) Waterhole use by African Fauna. *South African Journal of Wildlife Research*, **42**, 117–127.

Hayward, M.W. & Kerley, G.I.H. (2009) Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation*, **142**, 1–13.

Hebblewhite, M. & Merrill, E. (2008) Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.

Hebblewhite, M. & Merrill, E.H. (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, **90**, 3445–54.

Hedenstrom, A. & Alerstam, T. (1995) Optimal Flight Speed of Birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **348**, 471–487.

Hedges, S. & Gunaryadi, D. (2010) Reducing human–elephant conflict: do chillies help deter elephants from entering crop fields? *Oryx*, **44**, 139.

Hetem, R.S., Maloney, S.K., Fuller, A. & Mitchell, D. (2014) Heterothermy in large mammals: inevitable or implemented? *Biological reviews of the Cambridge Philosophical Society*.

Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouché, P., Ipavec, A., Convers, A., Ombredane, D. & Visscher, M.-N. (2010) Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodiversity and Conservation*, **19**, 2003–2024.

Hillman, J.C. & Hillman, A.K.K. (1977) Mortality of wildlife in Nairobi National Park, during the drought of 1973–1974. *African Journal of Ecology*, **15**, 1–18.

Hobbs, R.J., Higgs, E. & Harris, J. a. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in ecology & evolution*, **24**, 599–605.

Hoglander, C., Dickson, B.G., Rosenstock, S.S. & Anderson, J.J. (2015) Landscape models of space use by desert bighorn sheep in the Sonoran Desert of southwestern Arizona. *The Journal of Wildlife Management*, **79**, 77–91.

Holdo, R.M., Dudley, J.P. & Mcdowell, L.R. (2002) Geophagy in the African Elephant in Relation to Availability of Dietary Sodium. *Journal of Mammalogy*, **83**, 652–664.

Holdo, R.M., Holt, R.D. & Fryxell, J.M. (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American naturalist*, **173**, 431–45.

Holdo, R.M. & McDowell, L.R. (2004) Termite Mounds as Nutrient-Rich Food Patches for Elephants. *Biotropica*, **36**, 231–239.

Hoskins, A.J., Costa, D.P. & Arnould, J.P.Y. (2015) Utilisation of Intensive Foraging Zones by Female Australian Fur Seals. *Plos One*, **10**, e0117997.

Houston, a. I. (2006) The flight speed of parent birds feeding young. *Journal of Avian Biology*, **37**, 545–554.

Hunter, C.G.G. (1996) Land uses on the Botswana / Zimbabwe border and their effects on buffalo. *South African Journal of Wildlife Research*, **26**, 136–150.

Illius, A.W. & O'Connor, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, 283–294.

Jachowski, D.S., Slotow, R. & Millspaugh, J.J. (2014) Good virtual fences make good neighbors: Opportunities for conservation. *Animal Conservation*, **17**, 187–196.

James, C.D., Landsberg, J., Morton, S.R. & others. (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments*, **41**, 87–121.

Jarman, P.J. (1973) The free water intake of impala in relation to the water content of their food. *East African Agricultural and Forestry Journal*, **38**, 343–51.

Johnson, D.S., Hooten, M.B. & Kuhn, C.E. (2013) Estimating animal resource selection from telemetry data using point process models. *Journal of Animal Ecology*, **82**, 1155–1164.

Jonsen, I., Flemming, J. & Myers, R. (2005) Robust state-space modeling of animal movement data. *Ecology*, **86**, 2874–2880.

Jönsson, P. & Eklundh, L. (2004) TIMESAT-a program for analyzing time-series of satellite sensor data. *Computers & Geosciences*, **30**, 833–845.

Kangwana, K. (2011) The Behavioral Response of Elephants to the Maasai in Amboseli. *The Amboseli Elephants A Long-Term Perspective on a Long-Lived Mammals* (eds C.J. Moss),, H. Croze), & P.C. Lee), pp. 307–317. The University of Chicago Press.

Kartzinel, T.R., Chen, P. a., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W. & Pringle, R.M. (2015) DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences*, **112**, 201503283.

Kay, R.N.B. (1997) Responses of African livestock and wild herbivores to drought. *Journal of Arid Environments*, **37**, 683–694.

Kinahan, A., Pimm, S. & van Aarde, R.J. (2007) Ambient temperature as a determinant of landscape use in the savanna elephant, Loxodonta africana. *Journal of Thermal Biology*, **32**, 47–58.

King, L.E., Douglas-Hamilton, I. & Vollrath, F. (2011) Beehive fences as effective deterrents for crop-raiding elephants: Field trials in northern Kenya. *African Journal of Ecology*, **49**, 431–439.

Kittur, S., Sathyakumar, S. & Rawat, G.S. (2010) Assessment of spatial and habitat use overlap between Himalayan tahr and livestock in Kedarnath Wildlife Sanctuary, India. *European Journal of Wildlife Research*, **56**, 195–204.

de Knegt, H.J., Langevelde, F. Van, Skidmore, A.K., Delsink, A., Slotow, R., Henley, S., Bucini, G., Boer, W.F. De, Coughenour, M.B. & Grant, C.C. (2011) The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, **80**, 270–281.

Kuiper, T.R., Loveridge, A.J., Parker, D.M., Johnson, P.J., Hunt, J.E., Stapelkamp, B., Sibanda, L. & Macdonald, D.W. (2015) Seasonal herding practices influence predation on domestic stock by African lions along a protected

area boundary. *Biological Conservation*, **191**, 546–554.

Landman, M., Schoeman, D.S., Hall-Martin, A.J. & Kerley, G.I.H. (2012) Understanding Long-Term Variations in an Elephant Piosphere Effect to Manage Impacts. *PLoS ONE*, **7**.

Lange, R.T. (1969) The piosphere: sheep track and dung patterns. *Journal of Range Management*, **22**, 396–400.

Langman, V. a, Roberts, T.J., Black, J., Maloiy, G.M., Heglund, N.C., Weber, J.M., Kram, R. & Taylor, C.R. (1995) Moving cheaply: energetics of walking in the African elephant. *The Journal of experimental biology*, **198**, 629–632.

Leblond, M., Dussault, C. & Ouellet, J.-P. (2013) Avoidance of roads by large herbivores and its relation to disturbance intensity (ed V Hayssen). *Journal of Zoology*, **289**, 32–40.

De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula, H.M., Heitko, I.M.A., Reid, R.S., De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula, H.M., Heitkonig, I. & Reid, R.S. (2001) Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation*, **100**, 297–306.

Leggett, K. (2006a) Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. *Pachyderm*, **40**, 24–34.

Leggett, K.E. a. (2006b) Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology*, **41**, 17–36.

Loarie, S.R., Aarde, R.J. Van & Pimm, S.L. (2009) Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, **142**, 3099–3107.

Loarie, S.R., van Aarde, R.J. & Pimm, S.L. (2009) Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, **142**, 3086–3098.

Loveridge, a. J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2006) Influence of drought on predation of elephant (Loxodonta africana) calves by lions (Panthera leo) in an African wooded savannah. *Journal of Zoology*, **270**, 523–530.

Macandza, V. a., Owen-Smith, N. & Cain, J.W. (2012) Habitat and resource partitioning between abundant and relatively rare grazing ungulates (ed V Hayssen). *Journal of Zoology*, **287**, 175–185.

Macandza, V. a., Owen-Smith, N. & Cain III, J.W. (2012) Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos*, **121**, 891–898.

Macron, C., Pohl, B., Richard, Y. & Bessafi, M. (2014) How do Tropical Temperate Troughs Form and Develop over Southern Africa? *Journal of Climate*, **27**, 1633–1647.

Maloney, S.K., Moss, G., Cartmell, T. & Mitchell, D. (2005) Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (Connochaetes gnou). *Journal of comparative physiology. A, Neuroethology, sensory, neural, and behavioral physiology*, **191**, 1055–64.

Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D. & Loison, A. (2014) Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biological Conservation*, **177**, 1–11.

Marshal, J.P., Rajah, A., Parrini, F., Henley, M., Henley, S.R. & Erasmus, B.F.N. (2010) Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. *European Journal of Wildlife Research*, **57**, 537–548.

Martin, J., Benhamou, S., Yoganand, K. & Owen-Smith, N. (2015) Coping with Spatial Heterogeneity and Temporal Variability in Resources and Risks: Adaptive Movement Behaviour by a Large Grazing Herbivore. *Plos One*, **10**, e0118461.

Matthiopoulos, J. (2003) The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, **159**.

McFarlan, D. & Wright, P. (1969) Water Conservation By Inhibition of Food Intake. *Physiology & behavior*, **4**, 95–&.

McLaughlin, R.L. & Montgomerie, R.D. (1989) Brood dispersal and multiple central place foraging by Lapland longspur parents. *Behavioral Ecology and Sociobiology*, **25**, 207–215.

Miguel, E., Grosbois, V., Caron, A. & Boulinier, T. (2013) Contacts and foot and mouth disease transmission from wild to domestic bovines in Africa. *Ecosphere*, **4**, 1–32.

Moss, C.J., Croze, H. & Lee, P.C. (2011) *The Amboseli Elephants A Long-Term Perspective on a Long-Lived Mammals*. The University of Chicago Press.

Moss, C.J. & Lee, P.C. (2011) Female reproductive strategies: individual life histories. *The Amboseli Elephants: a long-term perspective on a long-lived mammal* (eds C.J. Moss),, H. Croze), & P.C. Lee), pp. 187–204. The University of Chicago Press.

Mueller, T., Selva, N., Pugacewicz, E. & Prins, E. (2009) Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist. *Ecography*, **32**, 345–353.

Murwira, A., De Garine-wichatitsky, M., Zengeya, F.M., Poshiwa, X., Matema, S., Caron, A., Guerbois, C., Hellard, E. & Fritz, H. (2013) Resource gradients and movement accross the edge of transfrontier parks. *Transfrontier conservation areas: people living on the edge* (eds J.A. Andersson),, M. De Garine-Wichatitsky),, D.H.M. Cumming),, V. Dzingirai), & K.E. Giller), pp. 123–136. Routledge, London and New York.

Myhrvold, C.L., Stone, H. a & Bou-Zeid, E. (2012) What is the use of elephant hair? *PloS one*, **7**, e47018.

Nagy, K.A. (1994) Seasonal Water, Energy and Food Use by Free-Living, Arid-Habitat Mammals. *Australian Journal of Zoology*, **42**, 55.

Naidoo, R., Du Preez, P., Stuart-Hill, G., Jago, M., Wegmann, M., Preez, P. Du, Stuart-Hill, G., Jago, M. & Wegmann, M. (2012) Home on the range: factors explaining partial migration of African buffalo in a tropical environment. *PloS one*, **7**, e36527.

Newmark, W.D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the Environment*, **6**, 321–328.

Odadi, W.O., Karachi, M.K., Abdulrazak, S. a & Young, T.P. (2011) African wild ungulates compete with or facilitate cattle depending on season. *Science (New York, N.Y.)*, **333**, 1753–5.

Ogutu, J.O., Reid, R.S., Piepho, H.-P., Hobbs, N.T., Rainy, M.E., Kruska, R.L., Worden, J.S. & Nyabenge, M. (2014) Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation*, **23**, 573–596.

Okello, M.M. (2010) Contraction of Wildlife Dispersal Area in Olgulului – Ololorashi Group Ranch Around Amboseli National Park, Kenya. *The Open Conservation Biology Journal*, **4**, 34–45.

Olff, H. & Hopcraft, J.G.C. (2008) The Resource Basis of Human- Wildlife Interaction. *Serengeti III Human Impacts on Ecosystem Dynamics* (eds A.R.E. Sinclair),, C. Packer),, S.A.R. Mduma), & J.M. Fryxell), pp. 95–122. The University of Chicago Press.

Olson, D. (ed). (2002) *Elephant Husbandry Resource Guide*. Allen Press, Lawrence, USA.

Olsson, O. & Bolin, A. (2014) A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia*, **175**, 537–548.

Olsson, O., Brown, J.S. & Helf, K.L. (2008) A guide to central place effects in foraging. *Theoretical population biology*, **74**, 22–33.

Owen-Smith, N. (1996) Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, **26**, 107–112.

Owen-Smith, N. (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical

ungulate, the greater kudu (Tragelaphus strepsiceros). *Journal of Zoology*, **246**, 183–192.

Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2267–2278.

Owen-Smith, N. & Martin, J. (2015) Identifying Space Use at Foraging Arena Scale within the Home Ranges of Large Herbivores. *Plos One*, **10**, e0128821.

Pangle, W.M. & Holekamp, K.E. (2010) Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. *Journal of Mammalogy*, **91**, 154–164.

Paper, O., Wittemyer, G., Getz, W.M., Vollrath, F. & Douglas-Hamilton, I. (2007) Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, **61**, 1919–1931.

Parker, G.E. & Osborn, F. V. (2006) Investigating the potential for chilli Capsicum spp. to reduce human-wildlife conflict in Zimbabwe. *Oryx*, **40**, 343.

Parkes, R., Halsey, L.G., Woakes, A.J., Holder, R.L. & Butler, P.J. (2002) Oxygen uptake during post dive recovery in a diving bird Aythya fuligula: implications for optimal foraging models. *The Journal of experimental biology*, **205**, 3945–3954.

Periquet, S., Valeix, M., Loveridge, A., Madzikand, H., Macdonald, D. & Fritz, H. (2010) Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour*, **79**, 665–671.

Perrotton, A. (2015) *Cattle Herding and Coexistence between Protected Areas and Their Periphery: A Participatory Approach to a Wicked Problem*.

Phillips, P.K. & Heath, J.E. (1992) Heat exchange by the pinna of the African elephant (Loxodonta africana). *Comparative biochemistry and physiology. Comparative physiology*, **101**, 693–9.

Phillips, P.K. & Heath, J.E. (2001) Heat loss in Dumbo: a theoretical approach. *Journal of thermal biology*, **26**, 117–120.

Polansky, L., Douglas-Hamilton, I. & Wittemyer, G. (2013) Using diel movement behavior to infer foraging strategies related to ecological and social factors in elephants. *Movement Ecology*, **1**, 13.

Polansky, L., Kilian, W. & Wittemyer, G. (2015) Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models. *Proc. R. Soc. Lond. B*, **282**.

Pretorius, Y., Stigter, J.D., de Boer, W.F., van Wieren, S.E., de Jong, C.B., de Knegt, H.J., Grant, C.C., Heitkönig, I., Knox, N., Kohi, E., Mwakiwa, E., Peel, M.J.S., Skidmore, a. K., Slotow, R., van der Waal, C., van Langevelde, F. & Prins, H.H.T. (2012) Diet selection of African elephant over time shows changing optimization currency. *Oikos*, **121**, 2110–2120.

Prins, H.H.T. (2000) Competition Between Wildlife and Livestock in Africa. *Wildlife conservation by sustainable use* (ed H.H.T. Prins), pp. 51–80. Springer Netherlands.

Redfern, J. V, Grant, R., Biggs, H. & Getz, W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, **84**, 2092–2107.

Roever, C.L., Beyer, H.L., Chase, M.J. & Van Aarde, R.J. (2014) The pitfalls of ignoring behaviour when quantifying habitat selection (ed N Roura-Pascual). *Diversity and Distributions*, **20**, 322–333.

Rowe, M.F., Bakken, G.S., Ratliff, J.J. & Langman, V. a. (2013) Heat storage in Asian elephants during submaximal exercise: behavioral regulation of thermoregulatory constraints on activity in endothermic gigantotherms. *The Journal of experimental biology*, **216**, 1774–85.

Rozen-Rechels, D., van Beest, F.M., Richard, E., Uzal, A., Medill, S. a & Mcloughlin, P.D. (2015) Density-dependent , central-place foraging in a grazing herbivore : competition and tradeoffs in time allocation near water. *Oikos*, 1–9.

Rubenstein, D.I. (2010) Ecology, social behavior, and conservation in zebras. *Advances in the Study of Behavior*, **42**, 231–258.

Ryan, S.J.S.J., Knechtel, C.U., Getz, W.M. & Science, E. (2006) Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management*, **70**, 764–776.

Scheibe, K.M., Eichhorn, K., Kalz, B., Streich, W.J. & Scheibe, a. (1998) Water consumption and watering behavior of Przewalski horses (Equus ferus przewalskii) in a semireserve. *Zoo Biology*, **17**, 181–192.

Scoones, I. (1995) Exploiting heterogeneity:habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments*, **29**, 221–237.

Scribner, S.J. & Wynne-Edwards, K.E. (1994) Moderate water restriction differentially constrains reproduction in two species of dwarf hamster (*Phodopus*). *Canadian Journal of Zoology*, **72**, 1589–1596.

Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. & Smith, R.J. (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, **15**, 776–783.

Shannon, G., Page, B.R., Duffy, K.J. & Slotow, R. (2006) The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia*, **150**, 344–54.

Shannon, G., Page, B.R., Mackey, R.L., Duffy, K.J. & Slotow, R. (2008) Activity Budgets and Sexual Segregation in African Elephants (Loxodonta africana). *Journal of Mammalogy*, **89**, 467–476.

Shrader, A.M., Bell, C., Bertolli, L. & Ward, D. (2011) Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica*, 1–8.

Shrader, A.M., Kerley, G.I.H., Brown, J.S. & Kotler, B.P. (2012) Patch Use in Free-Ranging Goats: Does a Large Mammalian Herbivore Forage like Other Central Place Foragers? *Ethology*, **118**, 967–974.

Shrader, A.M., Kotler, B.P., Brown, J.S. & Kerley, G.I.H. (2008) Providing water for goats in arid landscapes: effects on feeding effort with regard to time period, herd size and secondary compounds. *Oikos*, **117**, 466–472.

Simpson, G. (2014) Identifying periods of change in time series with GAMs, http://www.fromthebottomoftheheap.net/2014/05/15/identifying-periods-of-change-with-gams/

Sinclair, A.R.E. (1977) *The African Buffalo A Study of Ressource Limitation of Populations I*.

Sitters, J., Heitkönig, I.M.A., Holmgren, M. & Ojwang, G.S.O. (2009) Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biological Conservation*, **142**, 738–750.

Slotow, R. (2012) Fencing for Purpose: A Case Study of Elephants in South Africa. *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* (eds M.J. Somers), & M.W. Hayward), pp. 91–104.

Smit, I.P.J., Grant, C.C. & Whyte, I.J. (2007) Landscape-scale sexual segregation in the dry season distribution and resource utilization of elephants in Kruger National Park, South Africa. *Diversity and Distributions*, 1–12.

Smith, B.W. & McManus, J.J. (1975) The effects of litter size on the bioenergetics and water requirements of lactating Mus musculus. *Comp Biochem Physiol A Comp Physiol*, **51**, 111–115.

Spinage, C.A. (1992) The decline of the Kalahari wildebeest. *Oryx*, **26**, 147–150.

Squires, V. (1976) Walking, Watering and Grazing Behaviour of Merino Sheep on Two Semi-Arid Rangelands in South-West New South Wales. *The Rangeland Journal*, **1**, 13–23.

Squires, V. & Wilson, A. (1971) Distance between food and water supply and its effect on drinking frequency, and food and water intake of Merino and Border Leicester sheep. *Australian Journal of Agricultural Research*, **22**, 283.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. (2002) Temporospatial Distributions of Elk, Mule Deer, and Cattle: Resource Partitioning and Competitive Displacement. *Journal of Mammalogy*, **83**,

229–244.

Thrash, I. & Derry, J.F. (2008) The nature and modelling of piospheres: a review. *Koedoe-African Protected Area Conservation and Science*, **42**, 73–94.

Usman, M. & Reason, C. (2004) Dry spell frequencies and their variability over southern Africa. *Climate Research*, **26**, 199–211.

Valeix, M. (2011) Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology*, **27**, 163–170.

Valeix, M., Chamaillé-Jammes, S. & Fritz, H. (2007) Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, **153**, 739–748.

Valeix, M., Fritz, H., Canévet, V., Le Bel, S. & Madzikanda, H. (2008a) Do elephants prevent other African herbivores from using waterholes in the dry season? *Biodiversity and Conservation*, **18**, 569–576.

Valeix, M., Fritz, H., Chamaillé-Jammes, S., Bourgarel, M. & Murindagomo, F. (2008b) Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data. *Animal Conservation*, **11**, 391–400.

Valeix, M., Fritz, H., Dubois, S., Kanengoni, K., Alleaume, S. & Saïd, S. (2007) Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. *J. Trop. Ecol.*, **23**, 87.

Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2009) Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, **63**, 1483–1494.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. & Madzikanda, H. (2008c) The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, **46**, 402–410.

Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, **144**, 902–912.

Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D.W. (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, **25**, 337–351.

Vanak, A.T., Thaker, M. & Slotow, R. (2010) Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, **143**, 2631–2637.

Vandewalle, M.E. & Alexander, K.A. (2014) Guns, Ivory and Diseas: Past Influences on the Present Status of Botswana's Elephants and their Habitats. *Elephants and Savanna Woodland Ecosystems*, First Edit (eds C. Skarpe),, J.T. du Toit), & S.R. Moe), Zoological Society of London.

Viljoen, P. (1989) Spatial distribution and movements of elephants (Loxodonta africana) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology*.

Voeten, M.M. & Prins, H.H.T. (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, **120**, 287–294.

Walker, B.H., Emslie, R.H., Owen-Smith, N. & Scholes, R.J. (1987) To Cull or Not to Cull : Lessons from a Southern African Drought. *Journal of Applied Ecology*, **24**, 381–401.

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V. & Douglas-Hamilton, I. (2013) Characterizing properties and drivers of long distance movements by elephants (Loxodonta africana) in the Gourma, Mali. *Biological Conservation*, **157**, 60–68.

Weir, J. (1972) Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos*, **23**, 1–13.

Weissenböck, N.M., Arnold, W. & Ruf, T. (2012) Taking the heat: thermoregulation in Asian elephants under different climatic conditions. *Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology*, **182**, 311–9.

Weissenböck, N.M., Weiss, C.M., Schwammer, H.M. & Kratochvil, H. (2010) Thermal windows on the body surface of African elephants (Loxodonta africana) studied by infrared thermography. *Journal of Thermal Biology*, **35**, 182–188.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, **13**, 265–286.

Western, D., Groom, R. & Worden, J. (2009) The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. *Biological Conservation*, **142**, 2538–2546.

Wiens, J.A. (1989) Spatial Scaling in Ecology. *Functional Ecology*, **3**, 385–397.

van Wilgen, N.J., Goodall, V., Holness, S., Chown, S.L. & McGeoch, M. a. (2015) Rising temperatures and changing rainfall patterns in South Africa's national parks. *International Journal of Climatology*, n/a–n/a.

Williamson, B.R. (1975a) The condition and nutrition of elephant in Wankie National Park. *Arnoldia*, **7**, 1–16.

Williamson, B. (1975b) Seasonal distribution of elephant in Wankie National Park. *Arnoldia*, **7**, 1–16.

Wittemyer, G. (2011) Family Elephantidae (Elephants). *Handbook of the Mammals of the World. Vol. 2. Hoofed Mammals* (eds D. Wilson), & R. Mittermeier), pp. 50–79. Lynx Edicions, Barcelona.

Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, **69**, 1357–1371.

Wittemyer, G., Polansky, L., Douglas-Hamilton, I. & Getz, W.M. (2008) Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proceedings of the National Academy of Sciences*, **105**, 19108.

Wood, S. (2006) *Generalized Additive Models: An Introduction with R*.

Young, K.D., Ferreira, S.M. & Van Aarde, R.J. (2009) Elephant spatial use in wet and dry savannas of southern Africa. *Journal of Zoology*, **278**, 189–205.

Young, T.P., Palmer, T.M. & Gadd, M.E. (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation*, **122**, 351–359.

SUMMARY

Water and forage are key non-substitutable resources for herbivores in arid and semi-arid ecosystems. The distribution of surface water determines the distribution and abundance of water dependent animal species: yet little is known about the processes involved at the individual level. Thirteen African savanna elephant family groups and ten bulls (Loxodonta Africana) were tracked with GPS collars within and on the outskirts of Hwange National Park, Zimbabwe. Elephants behave as multiple central place foragers: They visit waterholes periodically every 5h, 24h, 48h or 72h and travel further from water during longer trips. During the dry season, temperatures increase and forage becomes depleted closer to water. Elephant family groups visit waterholes more often by increasing the proportion of briefer trips and abandoning 72h trips. However, they forage further during 24h trips by increasing travelling speed. Elephant movement patterns reveal that locomotional and navigational abilities are at the core of their coping strategies although these abilities are seldom allowed to vary in most foraging models of animal's use of heterogeneously distributed resources. During these foraging trips, family herds select areas with low waterhole density at multiple scales. Selection strength for low density areas increases with both distance to water and the advancement of the dry season. While scaling effects are widely recognized, the effects of the spatial distribution of multiple central places constraining foraging have been ignored although they determine depletion effects and their feedbacks on habitat selection. I also showed that elephant and buffalo strongly avoid livestock and people that herd them at the boundary of a protected area during the rainy season. Nevertheless, avoidance decreases during the dry season when foraging and drinking resources become scarce. Elephants are increasingly constrained by surface water availability during the dry season as their drinking requirements increase while they strive to maintain their forage intake. This study provides quantitative assessment of individual water dependence and of landscape effects of surface water distribution on a large herbivore. These findings can inform surface water management in contexts of aridification resulting from climate change.

RESUME

L'eau et le fourrage sont deux ressources non substituables pour les herbivores dans les écosystèmes arides et semi-arides. La distribution spatiale de l'eau de surface détermine la distribution et l'abondance des espèces dépendantes de l'eau. Cependant les processus impliqués à l'échelle individuelle demeurent méconnus. Treize groupes familiaux d'éléphants d'Afrique (Loxodonta africana) et dix mâles ont été équipés de colliers GPS dans le parc National de Hwange, au Zimbabwe, et à sa périphérie. Les éléphants fourragent autour de multiples points centraux : ils visitent un point d'eau périodiquement toutes les 5h, 24h, 48h ou 72h et s'éloignent plus de l'eau lorsque ils font des trajets de plus longue durée. Pendant la saison sèche, la température augmente et les ressources fourragères s'épuisent à proximité de l'eau. Les groupes familiaux d'éléphants visitent les points d'eau plus souvent en augmentant la fréquence des trajets courts et en abandonnant les trajets de 72h. Néanmoins, ils parviennent à se rendre plus loin de l'eau pendant les trajets de 24h en augmentant la vitesse de déplacement. Ainsi les patrons de déplacement révèlent que les capacités de locomotion et de navigation des éléphants sont au cœur de leur stratégie d'adaptation à la saison sèche. Malgré cela, ces capacités sont rarement incluses dans les modèles d'approvisionnement dans des environnements hétérogènes. Pendant ces trajets, les groupes familiaux sélectionnent les zones de faible densité de points d'eau à des échelles multiples. La force de la sélection pour ces zones de faible densité augmente avec la longueur du trajet et au cours de la saison. Bien que l'importance des échelles spatiales soit bien établie dans la littérature, les contraintes associées à l'utilisation de multiples points centraux distribués de manière hétérogène dans le paysage ont été négligées alors que cette distribution détermine le degré d'épuisement des ressources fourragères et les rétroactions sur la sélection de l'habitat. J'ai également montré que les éléphants et les buffles évitent fortement le bétail et les humains qui les conduisent en périphérie d'une zone protégée pendant la saison des pluies. Cependant cet évitement décline au cours de la saison sèche en raison de l'assèchement des points d'eau et de la raréfaction des ressources fourragères. Les éléphants sont de plus en plus contraints par la distribution de l'eau de surface en saison sèche en raison de l'augmentation de leur besoins en eau tandis qu'ils tentent de maintenir leur approvisionnement en fourrage. Cette étude donne une évaluation quantitative de la contrainte en eau à l'échelle individuelle ainsi que les effets de la distribution en eau dans le paysage sur un grand herbivore. Ces résultats peuvent guider les politiques de gestion de l'eau dans un contexte d'aridification dû au changement climatique.